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PRUNING TRIALS WITH LAXTON'S SUPERB APPLE

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RECENT pruning trials with the apple varieties Cox's Orange Pippin and Worcester Pearmain were reported when the trees were seven years old (Preston, 1954a). The present report, on trials with Laxton's Superb, has been deferred until more crop records were available so that the effects of pruning treatments on the biennial bearing habit of this variety could be considered.

Two tree shapes, open-centre and delayed open-centre, were tested and three pruning methods, renewal (Thompson, 1949), established-spur (Grubb, 1932), and regulated (Preston, 1954b). The pruning terms used in this paper are those defined and recommended by the Horticultural Education Association (1955).

MATERIAL AND TREATMENTS.

There were four separate trials of Laxton's Superb with trees on two rootstocks, the vigorous M.II and the less vigorous M.IV, and with two soils, the Malling Series of sandy-loam texture, here called loam for brevity, and the Lowlands Series of loamy-sand texture, here called sand (Preston and Stanton, 1947 ; Furneaux, 1954).

Trial 1, on loam. Trees were on M.IV at 18×20 feet. Single trees receiving each of the following treatments were distributed within twenty randomized blocks : open-centre, established-spur pruning ; delayed open-centre, established-spur pruning; regulated.

Trial 2, on sand. Trees were on M.IV at 18 feet square. Single trees receiving the same treatments as in Trial 1 were distributed within sixteen randomized blocks.

Trial 3, on loam. Trees were on M.II at 18×20 feet. Single trees receiving each of the following treatments were distributed within twelve randomized blocks : open-centre, established-spur pruning ; open-centre, renewal pruning ; delayed open-centre, renewal pruning ; delayed open-centre, established-spur pruning ; regulated.

Trial 4, on sand. Trees were on M.II at 18 feet square. The same treatments were used as in Trial 3 with the exception of regulated pruning. There were two trees under each treatment within each of six randomized blocks.

In Trials 1 and 2 the rows of Laxton's Superb alternated with Worcester Pearmain; in Trials 3 and 4, with rows of Cox's Orange Pippin.

Tree shaping.

Open-centre. The trees were headed back to a height of 30 inches at planting and any feathers were removed. The primary branches were limited to three ; these had their leaders tipped to obtain a secondary branch framework. Leader tipping was continued and inward growing shoots were removed, so building an open-centre shape.

Delayed open-centre. The trees were headed back to 33 inches at planting and feathers were removed. By notching and leader tipping, successive tiers of framework branches were formed around a central leader over a period of years. These

framework branches were not allowed to fork. When the trees were seven years of age the central leader was cut back into three-year-old wood to a framework branch.

Pruning methods.

Established-spur pruning. Leader tipping was relatively light with this vigorously growing variety. Very vigorous laterals that were not required for new branches were cut out. Very weak ones were cut back to 3 inches to form induced spurs. Laterals of medium vigour were left uncut to fruit ; these laterals, mainly on the outside of the tree, were shortened back later either to a spur or to a new lateral that had formed on them. Weak laterals from spur systems and induced spurs were shortened to 1 inch.

Renewal pruning. Leader tipping was light and was discontinued after the ninth year on trees on the loam, except for replacement leaders. About one-third of the one-year laterals were shortened each year to 2 or 3 inches to provide more laterals and the remainder were left uncut. About half the two-year laterals were left uncut and the others were shortened so as to leave about eight fruit buds on each. Most three-year laterals were stubbed after fruiting to produce more one-year laterals but some were cut back to a strong lateral that had grown out.

Regulated pruning. The trees were headed back to 30 inches at planting and feathers were removed. The number of primary branches was not restricted and during the next two years no more than three leaders were tipped each year ; leader tipping then ceased. Laterals were neither spur pruned nor shortened ; but crowded, thin and weak ones, irrespective of age, and also those that competed with the unpruned leaders, were removed completely.

The fruits were not thinned on any trees in the trials and axillary blossoms were allowed to remain.

Results.

Vigour.

The statistical analyses on data of shoot growth and trunk girth were carried out on their logarithms. The significant differences are expressed as significant ratios when the figures are transformed back again.

New shoot growth was measured during the first six years. Established-spur-pruned trees produced most shoot growth, except in Trial 4 on the sandy soil, where there was no significant difference between treatments (Table I). This was probably

Table I.

Total shoot growth (metres) per tree, 1946–51.

Trial	Soil	Rootstock	Pruning method			Sig. ratio (P=0·05)	
			Established-spur	Renewal	Regulated		
1	Loam	M.IV	273	—	123	1·27	
2	Sand	,,	171	—	93	1·31	
3	Loam	M.II	265	214	188	1·25 (12 : 24)	1·20 (24 : 24)
4	Sand	,,	56	70	—	n.s.	

due to the harder pruning required by the renewal-pruned trees to maintain shoot growth under the poor growing conditions on the sandy soil. Tree shape had no significant effect upon shoot growth ; in consequence in Trial 3, two significant ratios are given, one applying to comparisons involving renewal and established-spur pruning treatments (24 : 24) and one comparing either of these with regulated pruning (24 : 12). This also applies to the significant differences in Table VII relating to biennial intensity.

Trunk girth, measured at 9 inches above the union, showed (Table II) that at 10 years of age established-spur-pruned trees on M.IV were larger than the regulated

TABLE II.

Mean trunk girth (cm.), trees 10 years old.

Trial	Soil	Rootstock	Established-spur	Regulated	Renewal	Sig. ratio (P=0·05)
1	Loam	M.IV	30·5	25·2	—	1·12
2	Sand	,,	24·5	22·2	—	n.s.
3	Loam	M.II	31·7	29·9	29·3	1·08 (12 : 24) 1·06 (24 : 24)
			Tree shape	Established-spur	Renewal	
4	Sand	M.II	Open-centre	16·6	20·9	1·21
			Delayed open-centre	20·0	18·1	

trees on the loam but there was no significant difference between treatments on the sand. Established-spur-pruned trees on M.II on the loam were larger than renewal-pruned trees, and regulated trees were intermediate. In Trial 4 on the sand, however, there was a significant interaction between tree-shaping treatments and pruning method. This was one of the few cases where a significant effect of tree shape was recorded.

Weight of prunings.

New and old wood were weighed separately. The weight of prunings from established-spur-pruned trees was greater than from other pruning treatments (Table III), again with the exception of Trial 4 on the sand where there was no appreciable difference between treatments.

The weight of prunings from trees on the loam was greater than from those on the sand, except for the regulated trees in Trials 1 and 2 where the differences were small. The difference in total weight of prunings removed from renewal-pruned and regulated trees in Trial 3 was small but there was a marked difference between the ratios of new to old wood removed from these two sets of trees. With regulated trees, over the trials as a whole, one pound of new wood was pruned away for every two pounds of older wood ; with renewal-pruned trees nearly an equal weight of both types of wood was removed ; with established-spur-pruned trees there were two pounds of new wood prunings for every pound of old wood prunings.

TABLE III.

Weight of prunings (lb.) per tree, 1950–54.

Trial	Soil	Rootstock	Pruning method					
			Established-spur		Renewal		Regulated	
			New wood	Old wood	New wood	Old wood	New wood	Old wood
1	Loam	M.IV	22·5	11·1	—	—	4·4	9·3
2	Sand	,,	16·0	9·5	—	—	5·8	10·6
3	Loam	M.II	26·8	13·6	12·3	15·1	7·2	17·1
4	Sand	,,	9·0	3·6	5·7	6·3	—	—
Ratio of new to old wood removed			2 : 1		1 : 1		1 : 2	

Fruit buds.

The number of fruit buds, recorded annually up to 1953, showed that many trees were in an " on " year phase while others were in an " off " phase within the same year. Regulated trees especially showed this effect. The reason for this is obscure, for it was not linked with earlier cropping.

Regulated trees formed most fruit buds and established-spur-pruned trees least (Table IV). In Trial 3, where all three pruning treatments can be compared,

TABLE IV.

Total number of fruit buds per tree, 1947–53.

Trial	Soil	Rootstock	Pruning method	Per cent. difference
1	Loam	M.IV	Regulated > established-spur	171
2	Sand	,,	,, > ,, ,,	194
3	Loam	M.II	,, > ,, ,,	230
			Renewal > ,, ,,	99
			Regulated > renewal	66
4	Sand	,,	Renewal > established-spur	88

regulated trees formed more fruit buds than did renewal-pruned trees. The harder cutting of the established-spur-pruned trees resulted in the annual production of new wood bearing axillary fruit buds whereas regulated trees bore axillary fruit buds biennially.

Total crop.

Over the trials as a whole, tree shape had no important effect upon yield. Regulated trees gave the heaviest yields (Table V). In Trial 1, however, the yield from the regulated trees did not differ significantly from that of delayed open-centre established-spur-pruned trees ; and in Trial 3 delayed open-centre renewal-pruned trees yielded nearly as heavily as the regulated trees.

The yields from trees on the loam were generally higher than those on the sand

TABLE V.

Total crop (lb.) per tree, 1948–55.

Trial	Soil	Rootstock	Established-spur		Renewal		Regulated	Sig. diff. (P=0·05)
			Open-centre	Delayed open-centre	Open-centre	Delayed open-centre		
1	Loam	M.IV	269	320	—	—	343	59·3
2	Sand	,,	194	186	—	—	305	68·8
3	Loam	M.II	326	312	322	392	419	79·2*
4	Sand	,,	109	129	209	150	—	74·9†

* Regulated *v.* renewal and established-spur. † Renewal *v.* established-spur.

but the difference between regulated trees on M.IV on the two soils was small. On the sand, trees on M.IV yielded more heavily than did those on M.II but on the loam the reverse was generally the case. It is not possible, however, to make a statistical comparison between trees on the different rootstocks or soils.

Fruit size.

The trees did not have their fruits thinned during the trials. Fruit size has been consistently larger from established-spur-pruned trees than from those under other treatments. Regulated trees gave the smallest fruits, though in this respect there was often little difference between regulated and renewal-pruned trees. Mean fruit size per tree has been expressed in number of fruits per pound, for two consecutive years, 1954 and 1955, when the trees were 10 and 11 years old (Table VI). These were both heavy cropping years. The figures provide a more realistic estimate of fruit size than would figures for the whole period of the trial, for the latter would

TABLE VI.

Fruit size ; mean number of fruits per pound, 1954–55.

Trial	Soil	Rootstock	Year	Established-spur		Renewal		Regulated
				Open-centre	Delayed open-centre	Open-centre	Delayed open-centre	
1	Loam	M.IV	1954	3·2	3·8	—	—	4·8
			1955	3·3	3·6	—	—	3·8
2	Sand	,,	1954	4·6	4·8	—	—	5·2
			1955	3·3	3·2	—	—	4·2
3	Loam	M.II	1954	3·7	3·8	4·7	5·0	5·1
			1955	3·3	3·3	4·1	4·4	4·1
4	Sand	,,	1954	3·8	4·0	4·6	5·0	—
			1955	3·5	2·3	4·6	3·0	—

include the early years when fruit size had not become a critical factor in relation to pruning method. Thinning would undoubtedly have improved fruit size on the regulated trees in many years but would not have been necessary with the established-spur-pruned trees.

Intensity of biennial bearing.

The intensity of biennial bearing of each individual tree was calculated from the number of picked and dropped fruits, over a period covering six pairs of years, i.e. 1948 and 1949, 1949 and 1950, and so on. Factor " I " (Hoblyn *et al.*, 1936) was used to measure the intensity of fluctuation in bearing ; it is arrived at by dividing the difference between consecutive pairs of years by their sum and multiplying by 100, 0 denoting equal numbers of fruits and 100 no fruits at all in alternate years. Shape of tree had no effect upon regularity of bearing, whereas method of pruning had a marked effect (Table VII).

TABLE VII.

Intensity of biennial fluctuation in number of fruits in terms of Factor I†, 1948–54.

Trial	Soil	Rootstock	Pruning method			Sig. diff. (P=0·05)	
			Established-spur	Renewal	Regulated		
1	Loam	M.IV	47	—	73	9·7	
2	Sand	,,	55	—	57	n.s.	
3	Loam	M.II	77	86	91	9·0 (12 : 24)	7·3* (24 : 24)
4	Sand	,,	71	70	—	n.s.	

* See p. 135. † Maximum 100.

On the loam, established-spur-pruned trees have been much less biennial than either regulated or renewal-pruned trees. But on the sand (Trials 2 and 4), there were no significant differences between pruning methods for intensity of biennial bearing. Although it is not possible to apply a test for significance, it is clear that trees on M.IV have been less intensely biennial than those on M.II on both soils and under different pruning treatments.

The biennial habit of Laxton's Superb and the reduction in intensity achieved by any one pruning method can be assessed by comparing Factor " I " for this variety with that for a regular bearing variety such as Worcester Pearmain. For comparable trees in Trials 1 and 2 the figures over the same period for Worcester Pearmain were :

	Established-spur	Regulated
Trial 1	32	35
Trial 2	38	39

Deblossomed trees.

A small number of trees under the three pruning treatments, adjoining and directly comparable with trees in Trial 3, were deblossomed by hand each spring for the first six years from planting. They were then allowed to crop.

Measurements of tree height and average spread, made during the winter before the deblossomed trees were allowed to crop and again four years later, showed that deblossomed established-spur-pruned and regulated trees were larger than comparable trees that had not been deblossomed but there was little difference in size for renewal-pruned trees.

The first crops, at seven years of age, from the formerly deblossomed established-spur and renewal-pruned trees were slightly less than the accumulated crops over the same period from normally treated trees, viz. by 35 and 13 lb. per tree respectively (Table VIII). The formerly deblossomed regulated trees, however, yielded 74 lb. per tree more fruit in their *first* year of fruiting than did the normally treated ones during their first *seven* years. The total yields from the formerly deblossomed trees for the four years to 1955 showed a slight increase for established-spur-pruned trees and a slight decrease for renewal-pruned trees compared with the yields from normally treated trees. The formerly deblossomed regulated trees, however, showed a crop increase of 32 per cent. over that from normally treated trees, due no doubt to their larger bearing surface. A similar result has been reported for trees of Cox's Orange Pippin treated in this manner (Preston, 1954a).

TABLE VIII.

Cropping (lb.) of normally treated and formerly deblossomed trees on M.II.

	Pruning method		
	Established-spur	Renewal	Regulated
Accumulated crop at 7th year from trees allowed to crop normally (1948-52)	84·8	125·4	150·4
First crop from formerly deblossomed trees in 7th year (1952)	49·6	112·1	224·6
Difference	−35·2	−13·3	+74·2
Total crop from normally treated trees, 1948-55 ..	325·6	321·6	419·3
Total crop from formerly deblossomed trees, 1952-55	337·1	306·4	554·9
Difference	+11·5	−15·2	+135·6
Biennial intensity (Factor I) for formerly deblossomed trees (maximum 100)	24	89	99

As might be expected, the biennial bearing index for formerly deblossomed regulated and renewal-pruned trees was high following a relatively heavy first crop ; but the index for established-spur-pruned trees was remarkably low (Table VIII). The first crop, therefore, from the formerly deblossomed established-spur-pruned trees did not result in serious biennial bearing in later years although it amounted to 58 per cent. of the accumulated crop borne by the normally treated trees. Furthermore, fruit size was very much better from the established-spur-pruned trees. When the crop was graded, 1·4 per cent. consisted of small fruits, 2–2¼ inches in size, from established-spur-pruned trees, whereas 40·9 per cent. of the crop from regulated trees consisted of small fruits.

DISCUSSION.

The established-spur method of pruning Laxton's Superb involved removal of a much greater proportion of new wood than did either the renewal or the regulated method. This stimulated new shoot growth, reduced the number of fruit buds, and lessened the intensity of biennial bearing in these trials.

The regular annual crops from established-spur-pruned trees were much smaller than the " on " year crops of the renewal-pruned and regulated trees ; in most cases the total fruit weight from the regulated trees was appreciably greater than that from other treatments. However, much of the fruit from regulated trees in the " on " year was small, especially that which set on one-year laterals, and this reduced the value of these heavier crops ; the fruit from established-spur-pruned trees was of good market size.

A severe frost, such as to cause complete loss of crop, has not occurred since these trees were planted. This would put all trees into a heavy " on " year in the following spring and provide a severe test as to whether established-spur-pruned trees can avoid the onset of intense biennial bearing. Meanwhile, evidence from trees that were completely deblossomed during their early years is encouraging. A relatively heavy first crop from these trees at seven years of age resulted in remarkably low biennial intensity (I=24) for established-spur-pruned trees in later years, compared with that for similarly treated renewal-pruned and regulated trees (I=89 and 99).

SUMMARY.

Winter pruning trials with the apple Laxton's Superb on M.IV and M.II, planted in 1945 on loam and sand soils, included open-centre and delayed open-centre tree shapes, and established-spur, renewal and regulated methods of pruning.

Established-spur pruning resulted in more new wood, a smaller number of fruit buds, good fruit size, and lessened the intensity of biennial bearing. Tree shape had little effect in these respects.

In general the regulated trees cropped much more heavily than the established-spur-pruned ones and the yield from renewal-pruned trees was intermediate, but there were several exceptions. On both soils trees on M.IV were less intensely biennial than those on M.II but it was not possible to test this statistically.

Some trees were deblossomed for six years and allowed to crop for the first time in the seventh year. This deblossoming increased tree size and resulted in little or no loss of total crop up to the eleventh year. The heavy first crop from formerly deblossomed established-spur-pruned trees did not result in serious biennial bearing in later years as was the case with renewal-pruned and regulated trees.

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TRIALS WITH MONURON FOR WEED CONTROL IN SOME DIRECT-SOWN VEGETABLE CROPS

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THE herbicidal properties of monuron, formerly known as CMU (3-(p-chlorophenyl)-1, 1-dimethylurea), were first described in 1951 by Bucha and Todd (1). This chemical was subsequently investigated primarily as a permanent soil sterilant for use on uncropped land, but it was also found in the U.S.A. to be promising as a residual pre-emergence herbicide for the control of annual weeds in certain vegetable crops (2). Trials were initiated in 1952 to determine the practical possibilities of monuron for selective weed control in vegetable and other crops under British conditions and the progress of this work was reported by Woodford (4). The present paper summarizes the results of further field trials with vegetable crops carried out during 1953 and 1954.

METHODS.

Most of the experiments were on a sandy loam at N.V.R.S. whilst two trials were carried out at each of the N.A.A.S. Experimental Horticulture Stations at Stockbridge House (Yorks.) and Efford (Hants.). They were of randomized block design with from three to six replicates and the plot size ranged from 2 to 24 square yards according to the type of experiment. A wettable powder formulation of monuron was applied as an aqueous suspension at 100 gallons per acre, before emergence of either weeds or crop, by means of a knapsack or small hand sprayer. Weed kills were assessed by counting survivors in a number of random quadrats when the initial kill was judged to be complete. The crop yield trials were harvested according to normal practice and the produce graded in the field as marketable or unmarketable.

RESULTS.

Susceptibility of annual weeds to monuron.

Several trials were carried out in which monuron at a range of dose rates was applied to a prepared seedbed in the absence of a crop, so that the effects on emergence and growth of annual weeds could be determined. The percentage kills were transformed to probit values, plotted against the logarithms of the application rates and regression lines were drawn in by eye judgment. From these, estimates of the rates required to kill 50 per cent. of the weed population were obtained and average values for eleven common species are shown in Table I. The rates necessary to kill 80 per cent. are also shown, since this figure approximates to a satisfactory practical degree of control.

It is clear that there was a considerable range in tolerance to monuron among the various species, some, for example *Capsella bursa-pastoris* (L.) Medic., being virtually eliminated by a rate as low as $\frac{1}{8}$ lb. per acre whereas others were unaffected by much higher rates. *Fumaria officinalis* L., *Veronica hederaefolia* L. and *V. persica* Poir. occurred in most of the trials and showed no sign of injury following application of 1 lb. per acre, whilst effects induced by higher rates were very slow in appearing. When observed until flowering, these species were sometimes found to be stunted on

TABLE I.

Relative susceptibility of some annual weeds to pre-emergence applications of monuron.

Species	Number of experiments	Average rate (lb. per acre) required to kill	
		50%	80%
Capsella bursa-pastoris (L.) Medic.	3	<0·13	<0·13
Poa annua L.	4	<0·13	0·17
Matricaria chamomilla L.	1	0·11	0·20
Thlaspi arvense L.	3	0·15	0·33
Raphanus raphanistrum L.	1	0·15	0·34
Chenopodium album agg.	11	0·15	0·34
Spergula arvensis L.	6	0·16	0·37
Stellaria media (L.) Vill.	4	0·20	0·42
Senecio vulgaris L.	2	0·28	0·45
Polygonum convolvulus L.	2	—	0·50
Polygonum aviculare agg.	6	0·53	1·12

plots treated with 2 lb. per acre, but for all practical purposes they were resistant to this rate. Seedlings of some other weeds were present in the trials in small numbers and it appeared that *Rumex crispus* L. and *Trifolium repens* L. were susceptible, *Atriplex patula* L. moderately so, but *Plantago major* L. was tolerant. The rates used in these trials had negligible effects on established perennial weeds.

Susceptibility of some vegetable crops to monuron.

In each of two seasons a trial was conducted in which single rows of ten crops, replicated six times, were sprayed with a range of dose rates of monuron immediately after sowing at the normal depths. Each crop was harvested as it reached maturity and the number of plants and total fresh weight for a unit length of row were determined. Dosage-response curves were constructed from these data and the values for the rates required to give a 50 per cent. response obtained by interpolation. These values are given in Table II, which illustrates two points. First, on the basis of susceptibility the crops appeared to be divisible into two groups, with onion, lettuce and radish more susceptible than the rest. Second, although this division was apparent in both seasons, the actual rates needed to give the 50 per cent. response were less in 1954 than they were in 1953.

A number of trials were carried out with some of the more tolerant crops in order to determine the effect of monuron on yield, both in the presence and in the absence of weeds. The results of two experiments with crops of red beet (globe) kept clean by hand-weeding are shown in Table III. In the 1953 trial, no adverse effects on the crop were apparent with rates up to $\frac{1}{2}$ lb. per acre of monuron. In 1954, however, $\frac{1}{2}$ lb. per acre reduced plant stand by a significant amount and the reduction in total root yield just reached significance ($P=0{\cdot}05$). In two other trials, summarized in Table IV, no hand-weeding of any of the plots was done. Monuron at rates of $\frac{1}{4}$ and $\frac{1}{2}$ lb. per acre killed a proportion of the weeds and resulted in a net increase in marketable yield. The higher rate of $\frac{3}{4}$ lb. per acre significantly reduced the crop stand in both trials.

TABLE II.

Relative susceptibility of some vegetable crops, sown at the normal depths, to sprays of monuron applied immediately after sowing.

Crop	Average rate (lb. per acre) required for 50 per cent. reduction in plant number and plant weight			
	1953		1954	
	Plant number	Fresh weight	Plant number	Fresh weight
Onion	—	—	0·2	0·1
Lettuce	0·5	0·5	0·3	0·1
Radish	0·5	0·4	0·2	0·1
Carrot	1·0	1·6	0·4	0·4
Parsnip	1·1	1·7	0·4	0·4
Spinach	1·6	1·7	0·6	0·3
Red beet (globe)	1·6	1·7	0·4	0·4
Pea	—	1·6	—	0·4
French bean	—	1·2	—	0·5
Broad bean	—	1·4	—	1·0

TABLE III.

Effect of pre-emergence applications of monuron on the yield of clean crops of red beet.

Treatment	N.V.R.S., 1953				N.V.R.S., 1954			
	Marketable roots per acre		Total roots per acre		Marketable roots per acre		Total roots per acre	
	Thousands	Tons	Thousands	Tons	Thousands	Tons	Thousands	Tons
Monuron—								
¼ lb. per acre	119	19·3	162	22·2	98	11·3	257	14·2
½ lb. ,, ,,	109	17·5	151	20·6	82	10·6	195	12·9
Control	106	17·3	148	19·9	112	12·0	267	15·2
Sig. diff. (P=0·05)	16	2·9	15	3·3	17	2·3	54	2·3

TABLE IV.

Effect of pre-emergence applications of monuron on the yield of weedy crops of red beet.

Treatment	Stockbridge House, 1954				Efford, 1954			
	Marketable roots per acre		Total roots per acre		Marketable roots per acre		Total roots per acre	
	Thousands	Tons	Thousands	Tons	Thousands	Tons	Thousands	Tons
Monuron—								
¼ lb. per acre ..	54	12·2	140	17·5	27	9·3	59	14·5
½ lb. ,, ,, ..	45	9·9	110	14·2	29	9·5	55	14·3
¾ lb. ,, ,, ..	31	7·2	79	10·7	23	7·2	47	11·0
Control	41	8·2	129	13·6	20	5·2	63	8·7
Sig. diff. (P=0·05)	13	3·7	29	4·8	8	3·1	8	3·7

Four trials with clean crops of peas are summarized in Table V. In three out of the four, monuron at $\frac{1}{4}$ lb. per acre had no significant effect on crop yield, whereas a rate of $\frac{1}{2}$ lb. per acre reduced the yield in all. When no weeding of the crop was done (last column of Table V), the injury to the crop was outweighed by the beneficial effects of lessened weed competition.

Table V.

Effect of pre-emergence applications of monuron on the yield of five crops of market-garden peas.

Treatment	Yield of marketable pods, tons per acre				
	N.V.R.S. (clean) 1953	N.V.R.S. (clean) 1954	N.V.R.S. (clean) 1954	Stockbridge (clean) 1954	Efford (weedy) 1954
Monuron $\frac{1}{2}$ lb. per acre ..	3·4	6·5	2·5	6·8	5·4
,, $\frac{1}{4}$ lb. ,, ,, ..	2·0	2·8	0·8	5·0	5·1
,, $\frac{1}{8}$ lb. ,, ,, ..	—	0·7	0·3	2·3	4·4
Control	3·4	6·5	3·5	6·8	4·4
Sig. diff. (P=0·05) ..	1·0	1·3	0·5	0·9	1·2

One trial with a clean crop of carrots was carried out in each season and the main results are shown in Table VI. In 1953, neither stand nor yield was adversely affected by rates of monuron up to $\frac{1}{2}$ lb. per acre. In 1954, on the other hand, plant stand was significantly reduced by the $\frac{1}{2}$ lb. rate and a rate of 1 lb. per acre had very severe effects both on stand and yield. No trials were done with weedy crops of carrots.

Table VI.

Effect of pre-emergence applications of monuron on the yield of clean crops of carrots.

Treatment	N.V.R.S., 1953 Total roots per acre		N.V.R.S., 1954 Total roots per acre	
	Thousands	Tons	Thousands	Tons
Monuron $\frac{1}{2}$ lb. per acre ..	538	30·1	899	26·1
,, $\frac{1}{4}$ lb. ,, ,, ..	560	32·4	772	24·0
,, 1 lb. ,, ,, ..	424	28·6	147	9·6
Control	569	31·1	988	28·8
Sig. diff. (P=0·05) ..	83	4·5	139	5·7

DISCUSSION.

Monuron is only slightly soluble in water and can be taken up from solution by roots and moved upwards in the plant. Injury to plants appears as a progressive die-back from the tips of the leaves, usually beginning with the older ones. Early work with this chemical in the U.S.A., summarized by McCall (2), showed that its efficiency as a herbicide was related to the type of soil. The most rapid and severe

effects appeared in plants growing on light, sandy soil, whereas the phytotoxicity was least on " muck " soils with a high organic content. It was also found that rainfall was important in determining the amount of injury to crops, because of the influence on the depth to which penetration into the soil occurred. Both factors have since been investigated by several groups of workers and their importance has been confirmed.

The present experiments were carried out on light soils with a relatively low organic matter content, so that the phytotoxic effects of monuron would be expected to be relatively severe. A comparison with the few other published results of trials in Britain suggests that this was the case. Both Parker (3) and Woodford (4) found that on heavier soils larger amounts of monuron were required to produce the same effects, although the relative susceptibility of the various species was similar.

The data of Table II show that, in the second season, damage to the crops appeared with lower application rates than in 1953. It would appear that this can be attributed to differences in the amount and distribution of rainfall during the period of crop growth, since the soil was similar in the two trials. In 1953 there were several weeks of fairly dry weather after spraying, whilst in 1954 the corresponding trial received 0·8, 1·4 and 1·0 inches during the first three weeks and the rainfall throughout the summer months was above average. In the wet season, the effect on plants increased very markedly with increasing application rate. Thus with red beet, pea and carrot, a rate of $\frac{1}{4}$ lb. per acre had no significant effect either on stand or on fresh weight at harvest, whereas $\frac{1}{2}$ lb. per acre reduced both to 30 per cent. of the control values. In the yield trials this was less marked but there was a general tendency towards greater crop injury during the wet season. It was noticeable in 1953 that the injurious effects of monuron were very slow to appear. In broad bean, for example, they were not seen until the pod stage, following heavy rain in July. The degree of weed control finally attained did not appear to have been greatly affected by differences in rainfall, although in dry conditions death occurred more slowly.

The data obtained for the various annual weeds demonstrate that there was a considerable range of interspecific tolerance to monuron. The three species *Fumaria officinalis*, *Veronica hederaefolia* and *V. persica* were outstanding in that they showed no injury, under a variety of conditions, as a result of applications sufficient to kill other species. This suggests that these species may have some degree of inherent, physiological tolerance to monuron. There was no indication of any similar degree of resistance in any of the crops investigated in these experiments. Onion, lettuce and radish were consistently the most susceptible, but none of the others exhibited consistent absence of damage when treated with monuron at $\frac{1}{2}$ lb. per acre, the minimum rate required to give acceptable control of the majority of annual weeds. Broad bean and French bean, the two crops least affected in 1953 (Table II), are both large-seeded and were accordingly sown deeply. Other observations indicate that the deep sowing was probably responsible for the high apparent resistance. It would appear, therefore, from the trials as a whole, that when crops were undamaged by rates of monuron sufficient to kill most of the weeds, the absence of injury was due to the herbicide remaining in the surface layers of the soil and not reaching the zone of absorbing roots. This is supported by many observations of the sudden appearance of characteristic injury symptoms at a late stage of growth shortly after heavy rain.

These experiments have not demonstrated that there is any appreciable degree of physiological tolerance to monuron in the crops investigated, but rather suggest that the selectivity sometimes achieved is based to a large extent upon physical factors. In the trials with red beet, pea and carrot, monuron at the rate of $\frac{1}{4}$ lb. per acre did not, with one exception, result in significant yield decrease and, when the crops were not weeded, yields tended to be greater than those of the unweeded control plots. The number of weed species which were effectively controlled by this rate was small, however, and the reduction in total weed number per unit area when the population consisted of several species was no greater than that which could be obtained by mechanical inter-row cultivation. It is clear from Table II that increasing the application rate to $\frac{1}{2}$ lb. per acre would involve a risk of severely reducing the crop stand if heavy rain occurred during the first few weeks after spraying.

The fact that the soil type has a large influence on the herbicidal action of monuron would present an additional complication in formulating general recommendations. Parker (3), working with sugar beet on light soils in 1954, obtained results very similar to those reported here for red beet in the same year. The rate of monuron which reduced the crop stand by 50 per cent. varied according to the soil moisture status but was of the order of $\frac{1}{2}$ lb. per acre. On heavy and peaty soils, however, he found that, while crop damage was greatly reduced, the control of weeds was also poor. Thus it appears that monuron would not be sufficiently reliable for use as a pre-emergence treatment in even the more tolerant of the crops investigated, since there would always be a risk of causing crop damage on the one hand or of obtaining poor weed control on the other.

SUMMARY.

1. Field experiments were carried out over two years to determine the response of vegetable crops and annual weeds to pre-emergence applications of monuron.

2. Monuron proved to be a potent herbicide and on light soils $\frac{1}{2}$ lb. per acre was sufficient to give more than 80 per cent. kill of some important annual weeds of vegetable crops. *Poa annua* and *Capsella bursa-pastoris* were the most susceptible species whereas *Fumaria officinalis*, *Veronica hederaefolia* and *V. persica* were resistant to rates of up to 2 lb. per acre.

3. Onion, lettuce and radish were the most readily killed of the vegetable crops; others, such as red beet and pea, withstood higher application rates. With all crops there were large differences in tolerance between the two seasons, thought to be associated with differences in the rainfall.

4. Trials with clean crops of red beet, pea and carrot showed that no serious yield reduction occurred as a result of applying monuron at $\frac{1}{4}$ lb. per acre. In wet conditions, rates of $\frac{1}{2}$ lb. per acre and above resulted in damage to the crops.

5. When crops of red beet and pea were not weeded, the beneficial effects of reduced weed competition on plots sprayed with monuron at $\frac{1}{4}$ lb. per acre outweighed any adverse effect of the herbicide on crop growth and resulted in yields greater than those of the unweeded control plots. Even on light soils with high rainfall, however, this rate did not lead to a commercially acceptable degree of control when the weed population was made up of several species.

6. It is concluded that, with the crops investigated, the degree of selectivity obtained was largely governed by physical factors. Because of the influence of rainfall and soil type, monuron appears to hold little promise as a reliable residual pre-emergence herbicide for these vegetable crops.

ACKNOWLEDGMENT.

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MOLYBDENUM AS A PLANT NUTRIENT

IX. THE EFFECTS OF DIFFERENT MOLYBDENUM AND MANGANESE SUPPLIES ON YIELD AND ON THE UPTAKE AND DISTRIBUTION OF MOLYBDENUM IN TOMATO PLANTS GROWN IN SAND CULTURE

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A NUMBER of independent investigations suggest that molybdenum and manganese are interrelated in their effects on the growth of plants. Thus manganese deficiency tends to cause accumulation of certain amino acids whereas, in the same plants grown with nitrate, molybdenum deficiency frequently causes decreases in amino acid concentrations (12), although deficiency of either element may result in nitrate accumulation. Manganese excess is known to induce iron deficiency in some plants. Thus, sugar beet, which is normally relatively tolerant of high manganese concentrations, shows marked chlorosis when high manganese is given in the presence of 5 p.p.m. molybdenum, a concentration which, if used alone, is ineffective in causing chlorosis (6) and is relatively harmless to most plants.

The effects of manganese level on molybdenum content, or vice versa, observed in a number of plants appear to be inconsistent and may depend upon the actual concentrations of these elements which were used, or upon other factors (2, 16, 20). There are also conflicting reports regarding the beneficial or unfavourable effects of molybdenum on growth when given in the presence of high levels of manganese. Thus molybdenum is considered to alleviate manganese-induced lower leaf scorch of flax (15) and is reported to be antagonistic to effects of manganese and other heavy metals in flax (14) in contrast to the results obtained with sugar beet (6). Molybdenum deficiency symptoms observed in plants grown in sand culture or in acid soils may be accentuated or modified by high manganese levels (2, 16).

The work described here was carried out in 1952 as part of a general programme begun in 1948 (12) to investigate interrelationships between molybdenum and other metals, including especially manganese. The immediate objective was to discover whether manganese supply affected the content or distribution of molybdenum in tomato plants grown in sand culture.

EXPERIMENTAL PROCEDURE.

Culture methods.

Tomato plants var. Market King were grown from seed sown in sand cultures. The general methods used, including those for the removal of molybdenum from the nutrients, have been fully described previously (5). Nitrogen was given as nitrate at 12 mg. eq./L. Molybdenum was given at 0·05 p.p.m. (Mo_2), or was omitted (Mo_1). The molybdenum level in the latter treatment was estimated to be the equivalent of 0·00001–0·000025 p.p.m. A third series in which molybdenum

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was given at 4·8 p.p.m. is also briefly noted later in one context. Manganese was given at 0·011 (Mn_1), 0·55 (Mn_2) and 11·0 p.p.m. (Mn_3) as the sulphate and this had been purified to remove molybdenum (5). The treatments began from the time of sowing, except that in the high manganese treatment the maximum level was given 25 days later to plants that had been grown at the normal level.

The cultures were arranged in two randomized blocks with a split plot layout in regard to molybdenum supply and were sampled to provide four replicates for analysis.

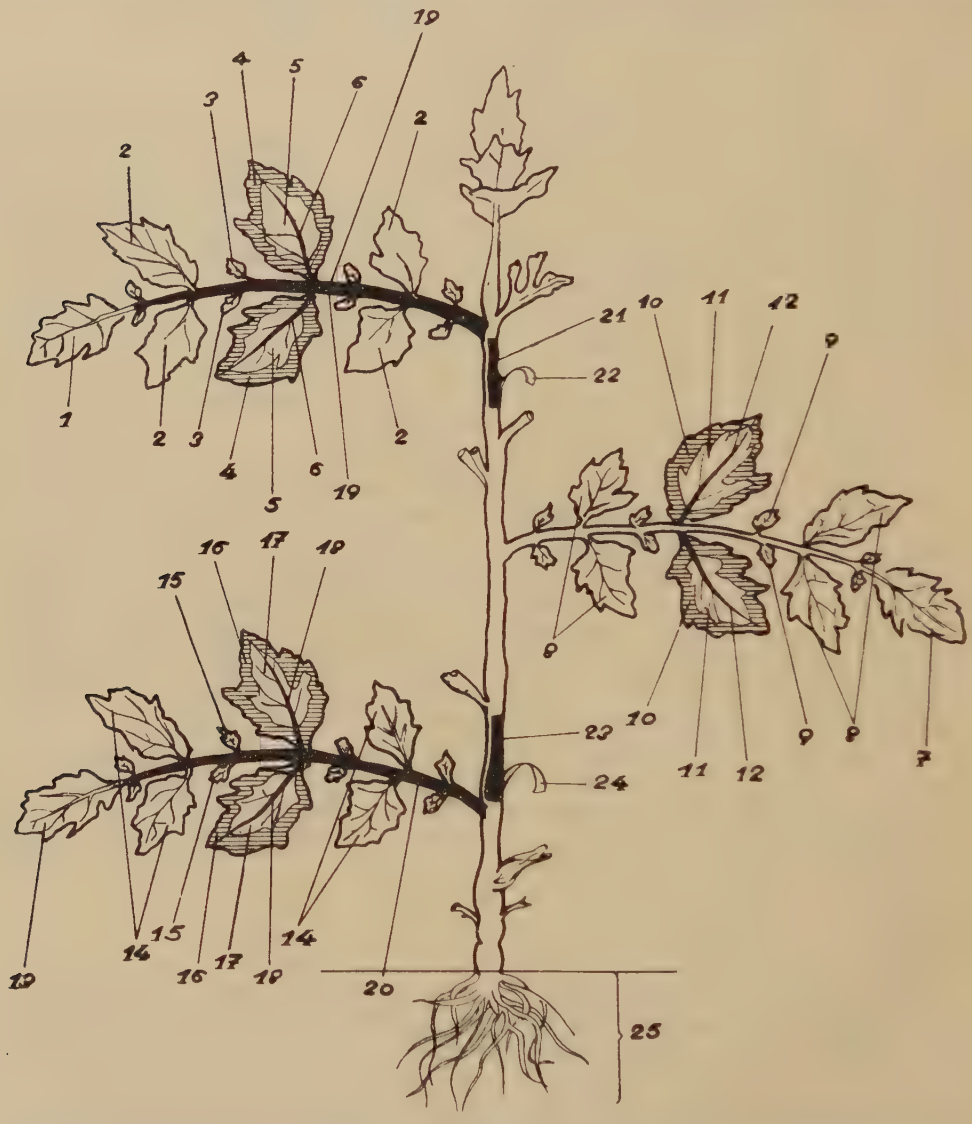

FIG. 1.
Diagrammatic illustration of sampling scheme used to provide material corresponding to index numbers and data in Table I.

Sampling.

Different stages of leaf growth in the same plant and different regions of the plant were sampled. The scheme is illustrated in Fig. 1 in which the numbers identify the stated regions for which the molybdenum contents are given in Table I. The lowest leaf shown in the figure corresponds with the oldest leaf on molybdenum-deficient plants that retained sufficient turgid tissue to permit the application of the sampling scheme illustrated; the highest leaf was uncurled and rapidly expanding; the remaining leaf was approximately mid-way between the others and almost fully expanded. The stem samples were obtained by peeling the outer layers from the vascular ring and corresponded to the epidermis and cortex in the outer sample and to vascular bundles and parenchyma in the inner sample. Molybdenum was estimated in dried material by an *Aspergillus niger* assay technique (11) in samples taken at 13 weeks.

The molybdenum concentration in leaf guttation fluid was also estimated as described by Hewitt and Hallas (11). Capillary collecting tubes, as illustrated in Fig. 2, were used to collect and accumulate droplets of guttation fluid from separate

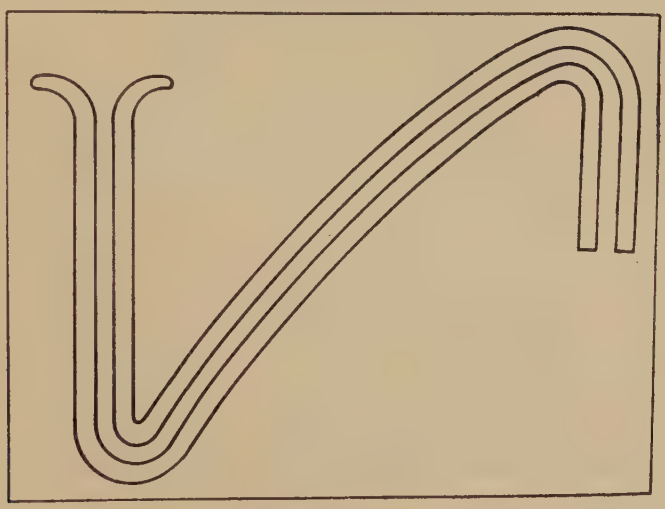

Fig. 2.
2 mm. capillary tube (drawn to scale) with funnel end used for collecting samples of leaf guttation fluid.

leaflets in each treatment at 8–9 a.m. after a night of high humidity. Their design permitted the collection in a few minutes of up to 400 mg. of fluid by touching lightly each guttation droplet with the inner surface of the funnel end of the acid-washed and dried tube which was weighed before and immediately after collection. The fluid, which generally weighed between 100 and 200 mg., was easily contained in the loop of the tube and was completely displaced and washed into the assay culture flask by a few drops of distilled water introduced into the funnel end. This arrangement ensured that no part of the tube in contact with the fluid was contaminated during handling, weighing or transfer.

TABLE I.

Molybdenum concentrations (p.p.m.) in dry matter in different parts, numbered as in Fig. 1, of tomato plants grown with different molybdenum and manganese supplies.

Plant sample (Fig. 1)		Mo_1 0·00001 p.p.m.			Mo_2 0·05 p.p.m.			Mean excluding Mo_1 Mn_3
		Mn_1 0·011 p.p.m.	Mn_2 0·55 p.p.m.	Mn_3 11 p.p.m.	Mn_1 0·011 p.p.m.	Mn_2 0·55 p.p.m.	Mn_3 11 p.p.m.	
Upper leaf								
Terminal leaflet	1	0·058	0·065	0·068	1·68	2·00	2·46	1·253
Apical and basal lateral	2	0·035	0·040	0·042	1·02	1·31	1·50	0·781
Minor lateral	3	0·027	0·032	0·036	0·83	0·94	1·11	0·588
Median margin	4	0·052	0·060	0·063	1·58	2·04	2·46	1·238
Median centre	5	0·061	0·068	0·072	1·68	2·16	2·69	1·332
Median midrib	6	0·009	0·011	0·013	0·24	0·30	0·33	0·178
Mean		0·040	0·044	0·049	1·17	1·46	1·59	0·861
Middle leaf								
Terminal leaflet	7	0·053	0·061	0·062	1·60	1·92	2·40	1·207
Apical and basal lateral	8	0·041	0·047	0·047	1·23	1·49	1·72	0·906
Minor lateral	9	0·024	0·030	—	0·89	1·02	1·23	0·639
Median margin	10	0·064	0·071	—	1·81	1·95	2·40	1·259
Median centre	11	0·062	0·070	0·059	1·81	1·99	2·41	1·268
Median midrib	12	0·012	0·017	—	0·38	0·47	0·54	0·284
Mean		0·043	0·049	—	1·29	1·44	1·78	0·920
Lower leaf								
Terminal leaflet	13	0·047	0·054	—	1·32	1·59	1·78	0·958
Apical and basal lateral	14	0·034	0·041	—	1·02	1·04	1·25	0·677
Minor lateral	15	0·030	0·032	—	0·82	1·02	1·22	0·624
Median margin	16	0·051	0·053	—	1·40	1·79	2·04	1·067
Median centre	17	0·063	0·070	—	1·78	2·10	2·60	1·323
Median midrib	18	0·003	0·009	—	0·22	0·25	0·35	0·166
Mean		0·038	0·043	—	1·09	1·30	1·54	0·802
Upper petiole	19	<0·005	<0·005	<0·005	0·11	0·15	0·20	0·094
Lower petiole	20	<0·005	<0·005	<0·005	0·14	0·20	0·20	0·110
Mean		<0·005	<0·005	<0·005	0·125	0·175	0·20	0·102
Upper stem								
Vascular bundles and parenchyma	21	0·018	0·021	0·022	0·50	0·70	0·91	0·430
Epidermis and cortex	22	<0·005	0·006	0·007	0·19	0·27	0·34	0·162
Lower stem								
Vascular bundles and parenchyma	23	0·020	0·026	0·030	0·69	0·93	1·14	0·561
Epidermis and cortex	24	0·018	0·022	0·028	0·52	0·74	0·92	0·444
Mean		0·015	0·019	0·022	0·475	0·66	0·83	0·400
Root	25	<0·005	<0·005	<0·005	0·43	0·52	0·59	0·310
L.S.D. between regions:								
5 per cent.		0·0042	0·0022	—	0·050	0·084	0·090	
1 per cent.		0·0057	0·0030	—	0·067	0·114	0·122	
0·1 per cent.		0·0077	0·0040	—	0·090	0·152	0·164	

Results.

Visual symptoms.

Molybdenum deficiency. Plants grown without added molybdenum showed moderate to severe symptoms of molybdenum deficiency (7, 10) at all manganese levels. These symptoms comprised paling and bright yellow interveinal mottling, usually of the oldest and later of the mid-stem leaves, followed by wilting, collapse and necrosis of the tissue. The necrosis usually appeared first at the tip of the terminal leaflet of an old leaf and later involved lateral leaflets of the same leaf and the terminal leaflets of the next younger leaf in a progressive manner from base to apex of the plant.

Effects of manganese supply and interrelationships with molybdenum. The appearance and incidence of symptoms in molybdenum-deficient plants was affected by the manganese supply and there appeared also to be a reciprocal effect of molybdenum supply on the appearance of manganese toxicity symptoms. The first signs of the mottling typical of molybdenum deficiency occurred 17 days from sowing, in plants of the Mo_1 Mn_2 treatment, and were followed several days later in plants of the Mo_1 Mn_1 treatment. Symptoms of molybdenum deficiency in the Mo_1 Mn_1 treatment thus appeared to be delayed or masked or to be less severe than in the Mo_1 Mn_2 treatment. Manganese deficiency (3) appeared to be the dominant effect for several weeks in the Mo_1 Mn_1 treatment until general recovery from manganese deficiency occurred, probably as a result of contamination. The distribution of symptoms was also noteworthy in plants in the Mo_1 Mn_1 treatment ; in these the oldest leaves tended to show typical manganese deficiency symptoms whereas somewhat younger mid-stem leaves showed the mottling and tip necrosis characteristic of molybdenum deficiency.

General leaf collapse and necrosis were increasingly severe with increasing manganese supply. The Mo_1 Mn_3 treatment produced also a necrosis in, or close to, the main veins of leaflets and on the stems in a manner similar to that described for manganese toxicity in tomato (4). This was accompanied by general yellowing of the older leaves which suffered a severe general collapse, thereby masking or modifying the effects of molybdenum deficiency in these regions. These changes occurred within two weeks of beginning the Mn_3 treatment and appeared to result from an interaction between high manganese and low molybdenum supply. Plants given the high manganese level without molybdenum were so severely injured that sampling of many parts was impossible.

The severity and time of appearance of manganese deficiency symptoms were similar in Mo_1 and Mo_2 treatments. It was concluded that molybdenum levels over the range tested did not affect manganese deficiency.

Plants in the Mo_2 Mn_2 treatment were normal. Those in the Mo_2 Mn_3 treatment were also normal in appearance for several weeks until the excess manganese level was doubled in the Mo_2 treatment later in the experiment, when slight symptoms of manganese toxicity (4) appeared. Old leaves also showed a chlorosis followed by necrosis between the veins and within the margins which remained green in leaflets of old leaves. These symptoms were suggestive of those commonly seen with magnesium deficiency in many plants (19). The relatively slight effects of manganese toxicity at the normal molybdenum level contrasted markedly with the severe effects observed in the molybdenum-deficient plants.

Yields.

Yields of whole plants and of fruit, as dry weight (Fig. 3), showed closely similar trends, being greatly decreased by molybdenum deficiency generally. Manganese excess caused a further decrease in yield in the low molybdenum but not in the normal molybdenum treatments. There was therefore an interaction between the manganese and molybdenum treatments. There was also a slight decrease in yield in the Mo_2 Mn_1 treatment and a slight increase in the Mo_1 Mn_1 treatment compared to the corresponding Mn_2 treatments. These differences, though not significant, possibly provide a further indication of an interaction between the effects of molybdenum and manganese on yield.

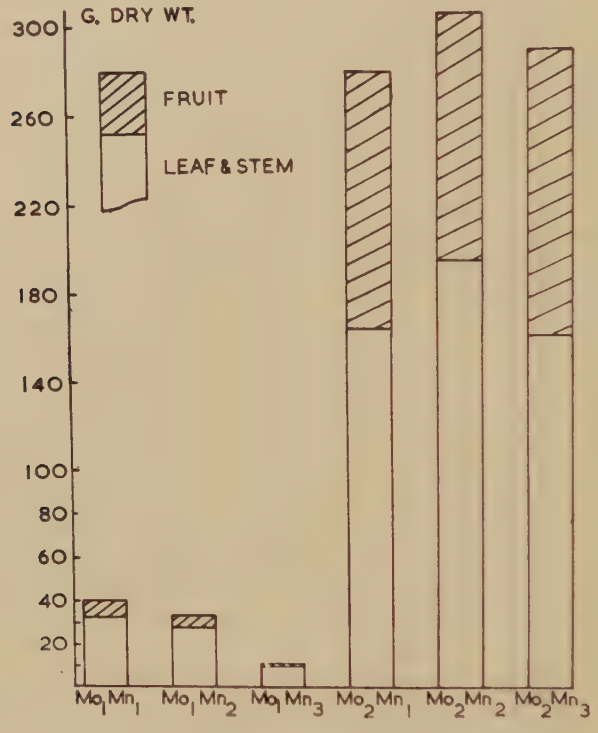

Fig. 3.

Yields of whole tomato plants grown at different molybdenum and manganese levels : Mo_1, 0·000025 p.p.m. approx. ; Mo_2, 0·05 p.p.m. ; Mn_1, 0·011 p.p.m. ; Mn_2, 0·55 p.p.m. ; Mn_3, 11 p.p.m.

Molybdenum content and distribution.

The concentration of molybdenum in different regions of the plants is shown in Table I. These are referred to by the number for each region shown in Fig. 1 and are grouped for convenience according to leaf age or stem position.

(i) *Effects of molybdenum and manganese levels.* The consistent increases in molybdenum concentration due to the increases in molybdenum supply were highly significant at 0·1 per cent. and were of the same order at each manganese level.

There was also a highly significant general *increase* in molybdenum concentration with increasing manganese supply. At the Mo_1 level the concentrations were greater in Mn_2 than in Mn_1 treatments for all regions except roots and petioles, significant at 0·1 per cent. for Nos. 1, 4, 5, 7, 8, 9, 10, 11, 13, 14, 17, 18 and 23 ; at 1 per cent. for Nos. 2 and 3 and at 5 per cent. for No. 24. There was a further increase, significant at 1 per cent., in molybdenum content of central parts of young median lateral leaflets, No. 5, and inner and outer old stem regions, Nos. 23 and 24, when manganese was increased from the Mn_2 to the Mn_3 level. At the Mo_2 level the molybdenum content increased steadily in all regions without exception, in the order $Mn_1 < Mn_2 < Mn_3$ with significance at 0·1 per cent. for Nos. 1, 2, 4, 8, 9, 10, 11, 13, 15, 16, 17, 21, 23, 24 ; at 1 per cent. for No. 3 and at 5 per cent. for Nos. 5, 7, 12, 14 and 18.

(ii) *Morphological distribution in regions of comparable age.* Comparisons between different regions of the same leaf age group showed that, for treatments Mo_1 Mn_1, Mo_1 Mn_2, Mo_2 Mn_1, Mo_2 Mn_2 and Mo_2 Mn_3, molybdenum content in each group usually increased in the following order in old and mid-stem leaves : median lateral midribs < minor lateral leaflets < apical and basal lateral leaflets < terminal leaflets < margins of median lateral leaflets < central areas of median lateral leaflets, i.e. :

$$6 < 3 < 2 < 1 < 4 < 5,$$
$$12 < 9 < 8 < 7 < 10 = 11,$$
$$18 < 15 < 14 < 13 < 16 < 17,$$

significant usually at 0·1 per cent. The same trends were observed in the Mo_1 Mn_3 treatment where only limited material was available.

Marginal and central areas of mid-stem leaflets, Nos. 10 and 11, did not differ significantly. In young leaves the order for the terminal leaflet, No. 1, and for margins of the median lateral leaflet, No. 4, was sometimes reversed. The values for young petioles, No. 19, were less than those for midribs in the same leaf, No. 6, in all the Mo_2 treatments, with significance at 0·1 or 1 per cent., and were also consistently lower than those for region 6 in the Mo_1 treatments for which all the values were very low. Differences were smaller for the comparison between the old leaf petioles, No. 20, and midrib, No. 18, but showed a similar trend in the Mo_2 treatments at lower significance. Vascular bundles and parenchyma of upper and lower stem regions, Nos. 21 and 23, consistently and significantly showed greater molybdenum contents than corresponding samples of epidermis and cortex, Nos. 22 and 24. The differences were relatively greater in the young part of the plants, Nos. 21 and 22, due to the low values in the outer, non-vascular tissues of this region, No. 22. Roots, No. 25, had concentrations significantly intermediate between stem parts, Nos. 22 and 24, in the Mo_2 treatments.

(iii) *Comparisons between similar morphological parts in different age groups.* Comparisons between corresponding parts of different ages revealed significant trends in molybdenum concentrations. The values for leaves as a whole (as means for all treatments and parts) decreased, with significance at 0·1 per cent., in the order : mid-stem, Nos. 7–12 > young, Nos. 1–6 > old, Nos. 13–18. Mean values for these

groups followed the same order in each treatment, usually with significance at 1 per cent. There was therefore a marked tendency for highest concentrations to occur in midstem leaves and for lowest in old leaves. The concentrations in terminal leaflets, however, decreased consistently and often with significance at 1 per cent. in the order : young, No. 1 > mid-stem, No. 7 > old, No. 13, leaves. With one exception in the $Mo_2 Mn_2$ treatment, the individual values for basal and apical lateral leaflets, margins and midribs of median lateral leaflets were greater in midstem leaves, Nos. 8, 10 and 12, than in old or young leaves, with significance at the 1 or 5 per cent. level. The means, for all treatments, of concentrations in these three parts decreased, usually with significance at 1 per cent., in the order : Nos. 1, 10 and 12 > 2, 4 and 6 > 14, 16 and 18 respectively. There was therefore a marked tendency for maximum concentrations to occur in midstem leaves and often for the lowest concentrations to occur in the old leaves.

(iv) *Molybdenum in leaf guttation fluid.* The molybdenum concentrations in samples of leaf guttation fluid are shown in Table II. In most instances they are the means for two samples. Data from plants given 4·8 p.p.m. Mo (Mo_3) are also included for comparative purposes. There were marked increases in the concentration with each increase in molybdenum supply. The concentration in guttation fluid

TABLE II.

Molybdenum content (p.p.m.) in leaf guttation fluid of tomato plants grown with different molybdenum and manganese levels.

Region sampled	Treatments						
	$Mo_1 Mn_1$	$Mo_1 Mn_2$	$Mo_1 Mn_3$	$Mo_2 Mn_1$	$Mo_2 Mn_2$	$Mo_2 Mn_3$	$Mo_3 Mn_2$
Upper leaves	0·0020	0·0026	0·0010	—	0·063	0·019	—
Lower leaves	0·0010	0·0010	0·0017	0·027	0·067	0·120	—
General	0·0024	—	0·0016	0·065	0·047	—	0·295
Mean ..	0·0018	0·0018	0·0014	0·046	0·059	0·070	0·295

was between about one-tenth and one-thirtieth that in dry matter in the Mo_1 series and between about one-thirtieth and one-fiftieth of that in dry matter in the Mo_2 series. The average dry matter contents of molybdenum-deficient and normal plants are about 11 and 14 per cent. of fresh weights respectively. Thus, compared with molybdenum concentrations in fresh tissue, the concentrations of molybdenum in guttation fluid ranged from equality to one-third in the Mo_1 series and from one-quarter to one-seventh in the Mo_2 series. The molybdenum concentration of 0·295 p.p.m. found in the guttation fluid from the Mo_3 series was only about one-thirtieth of that in fresh tissue given that level of molybdenum (unpublished data).

The effects of manganese level on the molybdenum content of guttation fluid were not clear-cut in the Mo_1 series but in the Mo_2 series the molybdenum concentration tended to increase with increase in manganese level.

DISCUSSION.

The relative distribution of molybdenum in dry material of different regions was practically independent of the molybdenum or manganese supply. The manner, already described, in which the withering symptoms of molybdenum-deficiency developed was consistent with the lower concentrations in old than in mid-stem leaves of deficient plants.

With the marked exception of the terminal leaflet, the concentrations in corresponding parts of young leaves of molybdenum-deficient plants were not greater than those found in the old leaves although the former did not show symptoms of molybdenum deficiency. This distinction in visual behaviour between the old and young leaves of deficient plants may be related to the fact that, whereas the older leaves were fully expanded, the young leaves were not.

The minor lateral leaflets, Nos. 3, 9, 15 (Fig. 1), which had generally lower concentrations of molybdenum than the terminal leaflets, Nos. 1, 7, 13, also did not show more pronounced deficiency symptoms than the others. The substantial difference in area between the young and old leaves is probably associated with differences in cell size and other developmental effects including senescence. It would thus appear that, in addition to molybdenum content, there may be other factors associated with leaf age or leaflet size which determine the sensitivity of tissues to molybdenum deficiency and these points merit further investigation.

The lower concentrations in petiole and midrib than in interveinal areas are consistent with the observations by Stout and Meagher (17) who found that radioactive molybdenum given to molybdenum-deficient tomato plants accumulated in interveinal areas; hence it is suggested that molybdenum is preferentially accumulated by mesophyll tissues. The autoradiographs shown by Stout and Meagher suggested also somewhat lower concentrations in margins than in mid-leaflet regions, a finding in agreement with results observed here. The distribution of molybdenum in stem regions confirmed the observations of Hewitt and Hallas (11) who found higher concentrations of molybdenum in vascular bundles than in cortex of cauliflower petioles, and of Hewitt and Agarwala (8) who observed highest concentrations in phloem of cauliflower petioles followed in decreasing order by endodermis, vascular parenchyma, cortex, xylem and epidermis.

The molybdenum concentrations in dry matter of various parts of plants given 0·05 p.p.m. were usually 30 times as great as in the plants given the low level. As the yields were nearly 7 times those of the deficient plants at both the normal and low manganese levels, the total molybdenum uptake was about 200 times greater in the normal than in the molybdenum-deficient plants. The efficiency with which the available molybdenum was absorbed was thus decreased by about fifteen-fold when the external concentration was raised by a factor of about 3,000. At the highest manganese level the total molybdenum uptake was about 550 times greater at the normal than at the low molybdenum level and the efficiency of absorption was therefore decreased by a factor of between 4 and 6 over the same molybdenum range.

The ratio of molybdenum concentration in guttation fluid to that present in the tissues or in the nutrient solutions also changed with changing molybdenum supply. In the Mo_1, Mo_2 and Mo_3 treatments the ratios of molybdenum concentrations in guttation fluid to those in the nutrient solutions were approximately 100 : 1, 1 : 1

and 0·06 : 1 respectively and the corresponding values for the ratios between molybdenum in guttation fluid and that estimated for fresh tissues were approximately 3 : 1, 0·3 : 1 and 0·03 : 1. The relative increases in the molybdenum exuded by guttation were considerably less, therefore, than the increases in the nutrient supply, or in the molybdenum present in the tissues, as a result of increased molybdenum supply.

Mulder (16) observed that in acid soils added manganese depressed the yield of cauliflower plants, accentuated molybdenum deficiency symptoms and decreased, though somewhat inconsistently, the molybdenum content of the plants. He also stated that in other experiments, whereas lettuce had shown similar responses to cauliflower, tomato and spinach which are both highly sensitive to molybdenum deficiency in soil or culture media (10, 13, 16) did not show these responses to added manganese ; further that in culture experiments cauliflower consistently failed to reveal evidence of the relationships he had observed in acid soils.

In our experiments manganese excess certainly decreased yields of tomato plants grown under molybdenum deficiency conditions, but did not do so appreciably at the normal molybdenum level. Plants given excess manganese at the low molybdenum level showed additional symptoms of injury which were distinct from those of molybdenum deficiency only and were also far more severe than those attributed to manganese toxicity in the plants given the normal molybdenum level. This observation is consistent with those of Millikan (14, 15) who concluded that the lower leaf scorch complex in flax which occurs in acid soils is the result of a high manganese—low molybdenum complex in which the addition of molybdenum mitigates the effects of the manganese excess.

Other experiments with cauliflower (E.J.H. unpublished) showed a marked reduction in severity of molybdenum deficiency and improved growth in cauliflower when manganese supply was decreased from normal to a level usually associated with manganese deficiency. Excess manganese accentuated injury by molybdenum deficiency and also induced modified symptoms. These effects are therefore analogous with those observed in tomato. The especially interesting point, however, is that in our experiment additional manganese over a range of 10^3 obviously *increased* the molybdenum content of both the molybdenum-deficient and the normal plants in practically all regions. The effects of manganese therefore outweighed the opposite effects of the accompanying sulphate ions which antagonize molybdenum uptake by tomato (18). The increase in sulphate concentration due to excess manganese was only 6 p.p.m. above the normal figure of 48 p.p.m. whereas the manganese level was increased by a factor of 20. It is noteworthy, however, that both the actual and the relative increases in average molybdenum content caused by increments in manganese supply were significantly less at the low than at the normal molybdenum level.

As the effects of increased manganese supply were clearly injurious, especially when molybdenum supply was insufficient, it must be concluded that some other effect of increased manganese supply was more injurious under molybdenum deficiency than under normal conditions, and this in spite of the compensating effects of relatively small increases in the very low molybdenum content of the plants. An explanation may be that, in plants grown with nitrate, manganese excess and molybdenum deficiency treatments *both* cause decreases in contents of certain free amino acids (9, 12 and unpublished data). The harmful effect of manganese excess

in further depressing already low amino acid concentrations in molybdenum-deficient plants (12) might thus outweigh the slight compensating effects of the observed increased molybdenum concentrations. Further investigations with more numerous levels of these elements are desirable to elucidate this point.

It is possible that in certain circumstances as, for example, in excised roots from which translocation cannot occur, the stimulatory effect of manganese on molybdenum uptake inferred here may be beneficial. This view may explain the observation by Hannay and Street (1) that added manganese caused increased growth, in White's medium containing glycine, of molybdenum-deficient excised tomato roots but was unfavourable in the presence of adequate molybdenum.

This discussion suggests that the molybdenum-manganese interaction comprises at least two components, namely : (i) greater metabolic injury by manganese excess in the absence of sufficient molybdenum than in the presence of an adequate supply, (ii) stimulation of molybdenum uptake in some plants by increasing manganese over a certain range. The overall effect may therefore depend on the relative importance of these two factors in different plants or in different circumstances.

SUMMARY.

1. Tomato plants var. Market King were grown in sand culture at low and normal levels of molybdenum and at low, normal and excess levels of manganese. The plants were divided into old, middle and young leaves, stems and roots, and leaves were further subdivided. Molybdenum was estimated in dried material and in guttation fluid by an *Aspergillus niger* assay method.

2. Yields were reduced by molybdenum deficiency. They were further reduced by the manganese excess level in the low molybdenum treatment, but not appreciably in the normal molybdenum treatment.

3. Molybdenum concentrations ranged from below 0·005 to 0·07 p.p.m. in molybdenum-deficient plants and from 0·11 to 2·60 p.p.m. in normal plants.

4. Mid-stem leaves contained, on the whole, higher molybdenum concentrations per unit of dry weight than either young or old leaves.

5. Terminal leaflets of old and mid-stem leaves contained less molybdenum than the largest median leaflets of the same leaves. Marginal areas of these leaflets contained less molybdenum than central interveinal areas and midribs contained least of all. Stems contained more molybdenum than midribs, petioles, or roots.

6. The distribution of molybdenum is consistent with the observation that deficiency symptoms appear in terminal leaflets of old leaves before they appear in those of median leaves. Other unidentified factors may determine the relative severity of symptoms in leaf tissues of comparable molybdenum status.

7. Progressively increasing manganese levels from 0·011 to 0·55 and to 11 p.p.m. caused highly significant *increases* in the molybdenum concentrations in most parts of the plants grown at both molybdenum levels.

8. It is concluded that the unfavourable effects of excess manganese on molybdenum-deficient plants, which have been observed here, are not due to changes in molybdenum content. The results, which are discussed in the light of other experiments, suggest that the inter-relationships between molybdenum and manganese in plant nutrition are probably complex or multiple in nature.

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ROOTSTOCKS FOR JAFFA AND JOPPA ORANGES*

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Long before the New World or Southern Africa was discovered, citrus was being grown in the countries bordering on the Mediterranean, mostly as seedlings in the gardens of the ruling classes. With the passage of time seeds of these trees were spread. When a world citrus industry started to expand some sixty years ago there existed in every citrus-growing country many orange seedlings of distinct horticultural groups of types, all of the same species *Citrus sinensis*, from selected trees of which further trees were propagated vegetatively for home and commercial planting.

Thus there originated many varieties, some of which are are closely related, belonging to one or another group. For instance, the Cadenera, one of the main varieties grown in Spain, is an improved seedless variety originating from the widespread Communa seeded orange, and in Israel the commercially grown Shamouti variety is an improved seedless selection of the common Belladi, which was originally grown from seed. Besides these dominant varieties, the Mediterranean countries were the home of many orange varieties and these were tried out commercially at one time or other during the early days of citrus growing in other countries, and especially in Florida and South Africa. Relatively few of them are being grown commercially today.

At one time the varieties named Joppa and Jaffa were regarded as distinct and were given detailed descriptions in text-books. There is, however, much confusion in the names applied to varieties or strains of midseason oranges that had been originally re-imported from the United States or imported direct from Mediterranean countries. Marloth and Basson (1955), in their discussion of midseason orange varieties, contended that, as far as South Africa is concerned, the names Joppa and Jaffa should be used only as referring to a type of orange having certain general characteristics. The adoption of the name " Jaffa " for South African midseason oranges of the Joppa-Jaffa type exported to the United Kingdom or the Continent is undesirable, as this word is used to advertise all oranges exported from Israel, although at first it was used only to distinguish their then dominantly grown variety, the Shamouti. Thus, either a distinct varietal name such as Tomango or the general term " Midseason " is in use.

The South African citrus industry is founded on the production of fruit for export, 94 per cent. of its production being oranges, practically all Navels and Valencias. In recent years great interest has been shown in the planting of orange varieties that mature between the Navel and Valencia seasons, thus giving a more continuous spread over the packing and marketing periods. According to the 1955 survey conducted by the field officers of the S.A. Co-operative Citrus Exchange, there are now 222,290 trees of " Other oranges ", mainly midseasons but excluding seedlings, in the orchards of exporting growers, an increase since 1950 from 2 per cent. to

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5 per cent. of the total number of orange trees in the Union. In view of the relatively greater planting rate and the heavy orders placed with nurserymen for midseason orange trees, this percentage is expected to increase still more.

Among the midseason orange varieties being planted commercially are some which originated in the Mediterranean and these must be classed as belonging to the Joppa or Jaffa group. One of the main characteristics of this group of oranges is that, when they are budded on rough lemon stock, a very distinct or marked union is formed. The tree has the appearance of having been girdled, with corky tissue on both stock and scion at the union, so that this usually shows a distinct ridge or swelling (Fig. 1a).

This marked girdling effect, which is very noticeable only with rough lemon as a rootstock, was first reported by Yedidyah (1937) with Shamouti orange in Israel and later attributed to a lack of affinity by Oppenheimer (1940) in his discussion of the rootstock problem for the Shamouti orange. As the vigour of trees when young was in no way impaired and high yields were obtained, Mendel (1956) does not accept this contention. The anatomical abnormalities of the wood and bark of trees in the rootstock plantings here reported are similar to the symptoms of the disease caused by the xyloporosis virus as summarized by Reichert *et al.* (1953) and to those shown by xyloporosis-infected sweet orange varieties budded on rough lemon in Florida, as described by Childs *et al.* (1956). The writer suggests that this girdling effect in certain Mediterranean varieties of oranges, most marked with the Joppa-Jaffa types when budded on rough lemon, is a virus reaction. This could be proved only by growing trees for a number of years in a greenhouse where they could not become infected with any form of virus, such trees to be propagated from virus-free material, raised from nucellar seed in the greenhouse, of both the rough lemon stock and the scion.

The following varieties in the Citrus Variety Orchard at Nelspruit give definite external signs of the reaction, varying from severe to slight : Addorosa (a Joppa selection), Cadenera (from Spain), Jaffa, Joppa, Malta Egg, Maltese Blood, Natal (from Brazil), Homosassa, Ruby Blood, Ruby Early, St. Michael's Blood, Shamouti, Tomango (a Jaffa selection), Verna (from Spain). The collection of varieties has not yet been subjected to the Orlando Tangelo test for the presence of the xyloporosis virus (Childs *et al.*, 1956) but the types of pitting recognized as symptomatic of this virus have been found on the wood of both stock and scion with these varieties. The three morphological forms of pitting (pits, striations and pin-points) associated by Reichert *et al.* (1953) with xyloporosis have been found with several other sweet orange varieties such as the Hamlin ; these, however, when budded to rough lemon, show no external signs at all of swelling or girdling at the union, even though virus is present, as indicated by the failure of this variety on sweet lime stock in the rootstock plantings.

The Shamouti is the main orange variety grown in Israel, being grown solely on two rootstocks. Trees on sweet lime are much affected by xyloporosis, come into bearing early, remain small, and decline at an early age. Trees on sour orange of local origin take longer to come into full bearing, grow larger and, although xyloporosis is present, do not show signs of undue decline. Reichert *et al.* (1953) described the effects of xyloporosis on the trees in the 18-year-old Mikve Israel trial in which 32 rootstocks were compared. They concluded that the selection of a suitable stock for the Shamouti orange depends mainly on its relationship to xyloporosis and

"little leaf", the productivity of the tree being dependent on the rootstock's susceptibility to the malady. They found that xyloporosis does not develop so readily on light soils so that, if early bearing is desired, sweet lime may be used as rootstock in such soils, although the life of the tree is shortened. The sour orange proved itself well as a stock, especially in the early years ; trees on Cleopatra mandarin performed well during the first ten years but declined rapidly after 18 years ; generally the rough lemon was a failure as a rootstock within ten years from planting, although up to 18 years its performance on light sandy soil was more satisfactory ; the nine varieties of sweet orange used as rootstocks gave especially good results, although some trees on two of them started declining after 6 years.

In considering these results it must be remembered that the tristeza virus, which kills sweet orange trees budded on sour orange and other stocks susceptible to this virus, has not as yet been reported from Israeli commercial citrus orchards, although shown to be present in an experimental planting of imported Meyer lemons.

SOUTH AFRICAN EXPERIMENTATION.

In his review of the citrus rootstock problem in South Africa the writer (1938) drew attention to the need to find a suitable rootstock for the Shamouti and other oranges of the Jaffa type. This need arose because, in commercial plantings, the performance of these varieties on rough lemon was unsatisfactory, trees remaining relatively small, having the girdling effect at the union and carrying fruit of relatively poor quality, especially during the early years of bearing. These factors no doubt helped to discourage growers from planting midseason orange varieties of this group.

Shamouti orange.

A preliminary planting of Shamouti orange on 12 rootstocks with 6 trees per combination was made in 1934, to which another 5 rootstocks were added in 1939. Buddings on grapefruit and yuzu failed in the nursery. Trees on dwarf rough lemon, dwarf sweet orange, *Citrus mitis* and Ethrog citron grew poorly and died within five years. Trees on Sampson tangelo, sweet lime and *Poncirus trifoliata* made poor growth and had totally declined within 10 years, while trees on sweet rough lemon, Japansche citroen, Natal naartje and Samboa (natural hybrid), after reasonable initial growth, started declining rapidly after 15 years. At 22 years, trees on rough lemon, Empress mandarin and four selections of sweet orange are in good health, except for two trees attacked by Dry Root Rot, and they bear heavy crops (Fig. 2).

No data are offered from this planting, which was made for observational purposes only. The various forms of pitting associated with xyloporosis were found to be present on all stock/scion combinations (Figs. 1a and 1b). A study of this material will be included in a paper by other workers on the occurrence of xyloporosis in South Africa.

Tomango orange.

Of the dozen or more oranges of the Joppa–Jaffa group under observation in the citrus variety orchard at Nelspruit, the Tomango, a midseason selection with very few seeds, already showed promise of being suitable for commercial planting some

20 years ago, mainly on account of its relatively high internal quality. This variety was therefore used in 1939 in a rootstock trial with 11 stocks replicated four times on sandy soil at Nelspruit. In order to reduce the coefficient of variability of the data to be obtained, especially in the early years of bearing, 4 trees planted at half the normal distance in the row were used per plot, alternate trees being removed at 12 years of age.

Growth.

Both grapefruit and *C. mitis* (Calamondin orange) failed as potential commercial stocks in the nursery; although the buds took, only runty budlings resulted. Budlings with *trifoliata*, sweet lime and Natal naartje were much smaller than the remaining combinations, but they appeared healthy and normal and so were included in the field trial. There was no statistically significant difference in the size, measured as trunk diameter, of the budlings on the other eight stocks.

During the first five years it was realized that sweet lime and *trifoliata* would produce only stunted trees and must be regarded as failures as rootstocks, and that Natal naartje was almost as bad. During this period trees on rough lemon, on Japansche citroen and, to some extent, on Empress mandarin grew more vigorously than those on sweet orange and came into bearing earlier. After ten years from planting, trees on Japansche citroen and sweet rough lemon began to lag behind the others in further growth and yield. At seventeen years trees on Empress mandarin were the largest and healthiest (Fig. 3); trees on the three sweet orange selections were large and healthy, though those on Waterkloof sweet orange were smaller than on the other two; trees on sweet rough lemon had a "pinched stock" effect and were only of medium size and with considerable die-back, while trees on Mazoe and Cairn rough lemon were large to medium with some die-back (Fig. 3); trees on Japansche citroen were only moderate in size with much die-back, and those on Natal naartje small and declining rapidly (Table I).

Xyloporosis.

The differences in tree size and rate of subsequent decline undoubtedly reflect differential effects of the xyloporosis virus—present in all the tops—on the different rootstocks. It is very likely that these effects are complicated by the presence of other viruses. The tristeza virus has been found in all sweet orange material examined from commercial orchards in South Africa and this, or a complex of viruses, might be responsible for the failure of grapefruit and *C. mitis* in the nursery and for the early failure of sweet lime, *P. trifoliata* and Natal naartje in the field.

Bark strips of only limited size could be removed from each tree in the rootstock planting for the purpose of observing the degree of xyloporosis as indicated by the presence of the various forms of pitting on the inner bark and trunk wood. So far as the limited material available showed, there was no association of a particular stock with different forms of pitting, all forms of pitting being found in varying degree, both on stock and on scion, on one or other of the trees of each stock/scion combination. Incidence was usually heavier on the scion. Although they showed many striations, trees on sweet orange and Empress mandarin were least affected. While the rootstock of trees on rough lemon was relatively free of pitting, the scions were pitted to an extreme degree (Fig. 1a).

Yield.

Very low yields were obtained from stunted trees on sweet lime, *trifoliata* and Natal naartje, viz. from 16 to 31 lb. per tree in the early years and only from 36 to 133 lb. when in full bearing, such yields being entirely uneconomic (Table I).

From the fifth to the seventh year after planting, yields from trees on rough lemon and Japansche citroen stocks were highly significantly ($P < 0{\cdot}01$) greater than those from trees on sweet orange and Empress mandarin, the average annual yields per tree being 84, 87, 41 and 55 lb. respectively. No significant difference was shown at this age between the three selections within each of the rough lemon and sweet orange groups.

However, the position changed entirely as the trees came into full bearing. From the twelfth to the sixteenth years after planting, the average annual yield per tree on Japansche citroen fell to the low level of 229 lb., that for sweet rough lemon to 278 lb., as against an average of 338 lb. for trees on the other two rough lemons. On Waterkloof sweet orange the yield was 292 lb. as against 398 lb. on Eloff sweet orange, while trees on mandarin averaged 391 lb. For this age period there was no significant difference in yield between trees on mandarin and sweet orange and rough lemon regarded as groups ; in the seventeenth year (1956), trees on Eloff and Bath's sweet orange significantly outyielded trees on Mazoe and sweet rough lemon, the respective yields being 480, 480, 319 and 268 lb. per tree. Within the groups, trees on Eloff and Bath's sweet orange significantly outyielded trees on Waterkloof and the declining trees on sweet rough lemon yielded significantly less than trees on Cairn rough lemon. (See Table I for variation in yield between selections within groups.)

Differences in yield due to stock effect are known to be affected by the type of soil on which the trees are grown. In the midseason orange variety trial at the Alkmaar Substation on medium clay loam soil (Marloth and Basson, 1955), Tomango orange trees on sweet orange stock gave 204 lb. of fruit per tree in their seventh year from planting, a crop which was significantly greater than the 172 lb. given by the same variety on rough lemon. Trees of the Shamouti variety, slower in coming into bearing, bore only 90 lb. of fruit, but trees on sweet orange had already caught up with those on rough lemon. Of other varieties of the Joppa–Jaffa group, such as Addorosa and Ruby Early, trees on sweet orange also outyielded those on rough lemon at this age.

That the Shamouti orange can bear heavy crops in later years in South Africa is shown by the performance of a tree of this variety (on sweet orange stock in the Nelspruit Citrus Variety Orchard) which in its twenty-second year yielded 977 lb. of fruit (Fig. 2).

Fruit size.

In any healthy tree there is usually a direct effect of amount of crop on fruit size, the larger the crop the smaller the fruit. Thus, when Marloth (1950) found larger fruit on heavier yielding trees of Valencia on rough lemon stock than on sweet orange, he concluded that this was a direct effect of rootstock on fruit size. Mendel (1956) also states that Shamouti trees on rough lemon stock have much larger fruit than trees on other stocks, but the relative size and yield of trees were not taken into account.

Marloth and Basson (1955) compared the relative fruit sizes of Joppa–Jaffa oranges from 7-year-old trees on sweet orange and rough lemon stocks in two years.

TABLE I.

Tomango orange rootstock planting at Nelspruit; planted 1939, 8 trees per stock.

Rootstock		Average yield per tree per year				Fruit quality, 4 years' average					Tree condition in 1956	
		1944–47	1951–55		1956	Rind thickness mm.	% Juice	T.S.S.	% Acid	Ratio	Relative size	Degree of decline
		lb.	lb.	Packed cases	lb.							
Sweet orange	Eloff	43	398	5¾	480	0·52	51	11·4	1·4	8·0 : 1	Large	Nil
	Waterkloof	40	292	4½	309	0·53	50	11·6	1·5	7·9 : 1	Medium	Slight
	Bath's	41	365	5½	480	0·52	51	11·4	1·4	8·2 : 1	Large	Nil
Rough lemon	Mazoe	77	312	4½	319	0·55	51	10·8	1·3	8·0 : 1	Medium	Medium
	Cairn	91	364	5½	397	0·55	48	10·8	1·3	8·3 : 1	Large	Slight
	Sweet	85	278	4	268	0·58	49	10·8	1·4	8·0 : 1	Medium	Marked
Empress mandarin		55	391	5¾	405	0·51	52	11·1	1·4	8·2 : 1	Large	Nil
Japansche citroen		87	229	3½	205	0·55	51	11·6	1·3	8·9 : 1	Med. small	Heavy
Average of 8 stocks		65	328	5	340	0·54	50	11·2	1·35	8·1 : 1	—	—
Significant difference	1% level	26	n.s.	—	138	n.s.	n.s.	0·7	0·12	—	—	—
	5% level	19	105	—	102	0·03	n.s.	0·5	0·09	—	—	—
Natal Tightskin naartje		17	133	2	73	0·53	49	11·5	1·5	7·6 : 1	Very small	Heavy
P. trifoliata		16	47	⅔	—	—	—	—	—	—	Runt	Dying
Sweet lime		31	36	½	—	—	—	—	—	—	Runt	Dead

the whole crop having been put over the grading table. In general, even though the trees on sweet orange bore heavier crops than those on rough lemon, the former gave an appreciably higher percentage of fruit of size 226* and larger. For Tomango orange trees the percentages were 47 and 21 on the respective rootstocks, for Addorosa 30 and 10, for Shamouti 71 and 64. (The 22-year-old Shamouti orange tree on sweet orange stock shown in Fig. 3 had 86 per cent. of its fruits of size 226 and larger.)

However, with the older Tomango orange trees at Nelspruit no consistent interrelation could be found between fruit size, stock, and yield for the 1956 crop. Trees on Eloff and Bath's sweet orange were equal in size and yielded the same, yet fruit from the former had 76 per cent. of size 226 and larger, while the latter had 56 per cent. With rough lemon stocks the percentage for the high-yielding trees on Cairn rough lemon was 70, that for declining trees on the Mazoe strain 80, and on the low-yielding sweet rough lemon 61. The average percentage for the trees on the three sweet orange stocks was 65, on the three rough lemons 69, and on mandarin 66. Medium-small trees on Japansche citroen, heavily infected with xyloporosis, gave a relatively low yield together with a marked decrease in fruit size, only 32 per cent. being of size 226 and larger.

Thus, on the evidence so far available, it cannot yet be stated that fruit size is directly dependent on the rootstock on which the tree is grown.

Fruit quality.

Details of quality of fruit from trees on the different stocks in the Nelspruit Tomango planting are given in Table I.

Fruit from trees on sweet orange and mandarin stocks had rinds significantly thinner than those of fruit from trees on rough lemon and Japansche citroen. Although differences in juice content could not be proven from the Nelspruit data, in the Alkmaar planting (referred to above) a significantly higher juice content was found in fruits from trees of Shamouti, Tomango, Ruby Early, and Addorosa varieties on sweet orange as compared with the same on rough lemon, the difference being as high as 6 per cent. in Shamouti and averaging 3 per cent. for 12 varieties. Fruit from trees on rough lemon stock contained significantly lower total soluble solids than fruit from trees on Japansche citroen and sweet orange, with that from Empress mandarin in between. At Nelspruit the respective percentages were 10·8, 11·5 and 11·1, but at Alkmaar, with young trees on heavy soil, the differences, although significant, were not so large. Also a slightly but significantly higher acid content of 1·4 per cent. for fruit on sweet orange stock as compared with 1·33 per cent. for fruit on rough lemon stock was found. Since both soluble solids and acid were higher for trees on sweet orange as compared with rough lemon, there was no difference in the resultant T.S.S. : acid ratio. The same was true for fruit trees on mandarin stock.

Although there have been many references over the years to the relatively poor quality of citrus fruits from trees on rough lemon as compared with fruit from trees on sweet orange and other rootstocks, especially when the trees were young and grown on light soils, Mendel (1956) was the first to offer statistical proof specifically for the Shamouti orange. He presented a complete review of the Mikve Israel Shamouti orange rootstock planting in respect of the influence of rootstock on trunk

* The number of fruit packed in a standard Californian box.

PLATE I

Fig. 1a.

Fig. 1b.

Fig. 1a.

Reaction of Tomango orange on rough lemon stock, tree 17 years old. Note girdling effect with corky tissue, swelling at union and deep pitting in wood.

Fig. 1b.

Reaction of Shamouti orange on Japansche citroen stock, tree 14 years old. Note striation pitting on both stock and scion, swelling at union and abnormal development of wood tissue into bark.

Fig. 2.

A magnificent tree of Shamouti orange on sweet orange stock, 22 years old. Average annual yield, over 1,000 lb. of fruit.

[face p. 168.

FIG. 3.

Tomango orange trees, 17 years old, each the best tree of four replicates. *Left :* on Empress mandarin stock ; yield, 522 lb. *Right:* on Mazoe rough lemon stock ; yield, 418 lb. Note the smaller tree and relative openness of foliage.

girth, top size, growth habit, health, yield, fruit size and fruit quality (colouring, peel thickness, juice, T.S.S., acid and ratio) for the years 1943–50. It would appear that these differences are far more pronounced with orange varieties of the Jaffa type than with standard varieties such as navels or Valencias, as Marloth's works have shown.

DISCUSSION.

It is becoming more and more apparent that one of the main problems of commercial production of citrus in all countries of the world is the increasing incidence of virus infection of the trees, as it results in retarded growth, lower yields of smaller fruit and shorter life of orchards. Until comparatively recently the problem of citrus rootstocks was regarded as being essentially one of physiological affinity or compatibility, ease of propagation of uniform trees, resistance of the stock to root and trunk diseases, adaptability to soil types, and the direct effect of the stock on the yield of the tree and the quality of fruit borne. To-day the overriding requirement is that the stock should suppress the deleterious effects of virus infection, though it must still conform to the older requirements of reasonable tree growth and longevity with good crops of high-quality fruit.

Further, the possibilities of selection within species of citrus rootstocks must be carefully investigated. Reichert *et al.* (1953) report the marked differences obtained with Shamouti orange budded to sour orange selections from local sources and from Baghdad, Brazil, Italy, Florida and California, all belonging to the species *Citrus aurantium* Linn. The writer has indicated repeatedly that significant differences are obtained from trees on different selections within the sweet orange and rough lemon groups. Special attention is now being devoted to this problem at the Nelspruit Station, with emphasis on the interrelationships with virus and virus complex infections.

In South Africa the sweet orange is gradually finding favour as a rootstock in preference to the hitherto invariably used rough lemon. Observations in the field over years, and the data herein reported, support the writer in unhesitatingly recommending sweet orange and definitely not rough lemon for use with oranges of the Joppa–Jaffa type. This applies to plantings on both light and heavy soils and, although the experimental plantings were made in the Eastern Transvaal, this recommendation is made for all citrus-growing areas of the Union. The two main factors taken into consideration are the relative susceptibility of trees on the two rootstocks to xyloporosis and the quality of fruit produced. Capital investment in citrus production is high, and the longer an established orchard stays in economical production the lower are the unit capitalization costs. With the great increase in potential production of citrus resulting from new plantings and the consequent increased competition in markets, not only in South Africa but all over the world, fruit quality must necessarily play a far more important rôle than it has in the past, and growers of fruit not up to the required competitive standard will undoubtedly experience difficulty in disposing of their product at remunerative prices.

The difference in performance of the Natal Tightskin naartje (tangerine) and the Empress mandarin (loose-skin naartje) as a rootstock for both Shamouti and Tomango oranges is striking, as both belong botanically to the same species, *Citrus reticulata* Blanco. It should be noted that the large-fruited Empress mandarin is

horticulturally a distinct variety from the Cleopatra mandarin, which is being used on an increasing scale in the United States as a rootstock on account of its resistance to the tristeza virus. The data offered here show that the Empress mandarin is a very promising rootstock for commercial citrus plantings of midseason oranges of the Joppa–Jaffa group. As a rootstock in the nursery it is not so easy to work with as rough lemon, being more difficult to bud, but it produces a far more extensive fibrous root system and is also deeper rooted. In the early years the yield of fruit from trees on this rootstock is almost as high as that on rough lemon and equals the best of all rootstocks when in full bearing. The fruit quality, even during early years of bearing, is excellent and in later years far excels that of fruit from trees on rough lemon.

Whether other varieties of loose-skin naartje will prove equally satisfactory as a rootstock has still to be shown, and trees for an experiment to test some 40 *C. reticulata* varieties and hybrids have already been propagated at Nelspruit. It is hoped that further trial plantings with Empress mandarin as a rootstock, and also with varieties other than midseasons, will be made by growers in different citrus-growing areas of the Union.

SUMMARY.

Midseason oranges of the Jaffa and Joppa types originating in the Mediterranean are being planted commercially on an increasing scale in the Union of South Africa. This paper reports the results obtained from investigations over twenty years with different rootstocks used for two of the varieties, the Shamouti and Tomango oranges. The relative incidence and deleterious effects of the xyloporosis virus in the tree are described and discussed.

The most suitable rootstock for both light and heavy soils was found to be sweet orange, while the hitherto unused Empress mandarin is indicated as a very promising stock to use for future plantings. Trees budded to rough lemon all show the characteristic marked corky girdling effect held to be associated with xyloporosis of these scion varieties at the bud union and, while yields on such trees are good for the first fifteen years of life, the fruit produced is of relatively poor quality, having a thicker rind, less juice and lower soluble solids than fruit from trees on sweet orange and Empress mandarin stocks. It is held that the new approach to citrus rootstocks investigation should be based primarily on a study of the relative susceptibility of the stocks to the expression of virus infection in the tree.

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OBSERVATIONS ON THE FRUITING HABIT OF THE RED RASPBERRY (*RUBUS IDAEUS* L.) AND ON AN OCCURRENCE OF CANE "DIE-BACK" IN SCOTLAND

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THE cane of the cultivated red raspberry is usually a biennial structure. Buds formed in the leaf axils during the first growing season produce in the following year the laterals that carry the flowers and fruit, after which the cane dies and is replaced by new growth from the stool. Previous studies on the differentiation of the buds in the first year (Waldo, 1933 ; Mathers, 1952) have shown that flower primordia are formed from mid- and late September onwards in Scotland and North America respectively, considerable development occurring in autumn but little between December and March. These studies, however, were apparently confined to the central axis of the main bud at each node, whereas it is known that some varieties, typically Lloyd George, usually bear two distinct buds at a node, the main (here termed primary) bud having just below it a smaller (secondary) bud which frequently produces a fruiting lateral, either accompanying that from the primary bud or replacing it after damage (Fig. 1).

The present study, at first concerned with the time of initiation of flowers on the central axes of secondary buds, showed that in the axils of the bud scales both of primary and of secondary buds there were still smaller buds (here termed tertiary) which, in some varieties, could initiate inflorescence primordia and sometimes form fruiting laterals. Of these buds, those in the outermost scale axils were always the most advanced in development. These observations led to a survey of the development of fruiting laterals in the field, in a range of varieties and over four seasons, and to an investigation of the effect of artificially shortening the laterals formed from primary buds. Observations were also made on an extensive "die-back" of second-year canes which occurred in one of the seasons.

In this paper the terms "primary lateral", "secondary lateral" and "tertiary lateral" denote laterals formed by direct extension of the axes of primary, secondary and tertiary buds respectively, and similarly the descriptions primary, secondary and tertiary are applied to the inflorescences formed on the three types of bud axis. It is realized that this terminology is arbitrary, but it is convenient. A typical arrangement of buds is shown diagrammatically in Fig. 2.

RESULTS.

OBSERVATIONS ON FLOWER INITIATION.

Buds from untipped maiden canes of Malling Landmark and Malling Notable (seventh-year stools) and Lloyd George (fourth-year stools), growing in a sheltered

* Resigned September, 1954.

garden at Dundee, were removed for dissection at about six-weekly intervals from 21st September 1952 to 21st March 1953. These varieties were used because their nodes normally carry both primary and secondary buds. Four pairs of buds, representing four roughly equal zones of the canes from base to tip, were taken from each variety on each date, the canes being chosen at random from a large number all well grown. The degree of development of each inflorescence was estimated from the condition of its oldest flower, the following arbitrary stages being used :

1, growing point of axis flattened but perianth not visible ;
2, perianth ring just visible ;
3, sepal rudiments formed ;
4, petal rudiments formed, sepals curving over torus, anther rudiments just visible ;
5, anther rudiments formed ;
6, carpels forming at base of torus ;
7, carpels half-way up torus ;
8, carpels three-quarters covering torus ;
9, carpels covering torus ;
10, carpels elongated and anthers lobed.

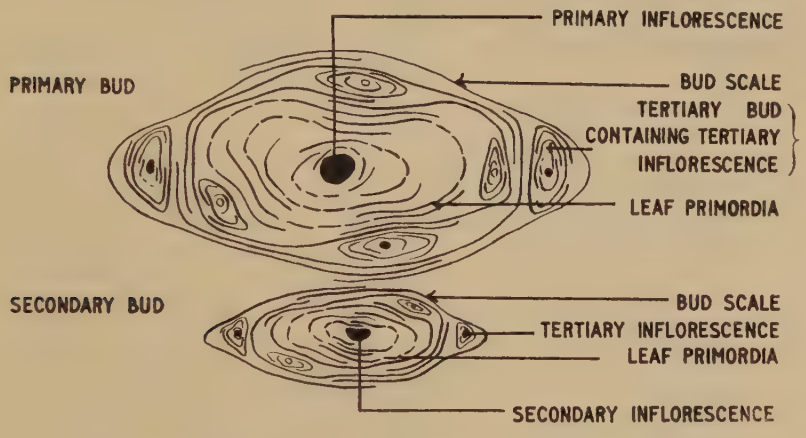

Fig. 2.
Cross-section showing primary, secondary and tertiary buds.

Table I, which summarizes the observations made, shows that all three varieties carried appreciable numbers of flower primordia on their primary and secondary inflorescences, but that tertiary inflorescences were more numerous in Lloyd George and Malling Notable (of which Lloyd George is a parent) than in Malling Landmark. Flower primordia were visible on all primary inflorescences in September and their subsequent development followed closely that described by Mathers (1952). The February and March dissections indicated a renewal, or increased rate, of flower initiation during those months. Secondary inflorescences generally had fewer flowers than primary ones and were later in development, whilst tertiary inflorescences were still smaller and less developed. Some, however, contained recognizable flower primordia in September.

TABLE I.

Raspberry bud development, 1952–53 ; 4 bud-pairs examined on each date.

Variety	Date	Primary inflorescence		Secondary inflorescence		Tertiary inflorescences on primary bud			Tertiary inflorescences on secondary bud		
		No. flowers	Stage	No. flowers	Stage	No.	No. flowers	Stage	No.	No. flowers	Stage
Lloyd George											
	21st Sept., 1952	7–8	3	3–5	2	3	2–5	1	1–2	1–3	1
	25th Oct., 1952	7–10	4	4–6	3	5–6	2–5	2–4	1–2	1–3	1–2
	20th Dec., 1952	8–9	5–7	4–6	3–4	5–7	2–6	3–5	1–2	2–4	2
	7th Feb., 1953	9–10	6–9	5–6	5	5	3–9	3–6	2	3–5	3
	21st March, 1953	13–18	10	5–8	6–8	5–7	2–6	3–7	2	3–4	3
Malling Notable											
	21st Sept., 1952	7–9	3	4–5	1–2	2–3	2–5	1–2	0	—	—
	25th Oct., 1952	6–11	3	5–6	1–2	3–6	2–5	1–3	0–1	2–3	2
	20th Dec., 1952	8–11	5	6–7	3–4	4–5	1–5	1–3	0–1	1–3	2
	7th Feb., 1953	9–10	5–6	6–8	3–4	2–4	2–6	1–3	1–2	2–4	3
	21st March, 1953	10–17	10	5–8	6–9	3–6	3–7	3–6	0–1	3–4	3
Malling Landmark											
	21st Sept., 1952	7–10	2	4–6	1–2	1–2	2–4	1–2	0	—	—
	25th Oct., 1952	6–9	2–3	4–7	2	0	—	—	0	—	—
	20th Dec., 1952	7–8	3–4	4–6	2–3	1–2	1–2	1	0	—	—
	7th Feb., 1953	7–11	3–4	6–7	2–3	0	—	—	0	—	—
	21st March, 1953	12–16	10	5–11	5–9	2–4	2–6	1–3	1–2	2–3	1

In March 1953 an assessment was made of bud development in canes of third-year stools of Malling Promise, Malling Jewel, Lloyd George and Norfolk Giant about to be used in an experiment, described below, on the effect of damage to primary laterals. Buds were examined from the upper, middle and basal zones of four canes of each variety, the rows having previously been tipped at 4¾ feet above ground level. The results from Lloyd George confirmed those given in Table I. Malling Promise, in contrast, carried no secondary buds at the nodes sampled, but it contained 1–4 tertiary inflorescences in all but its lowermost primary buds. Malling Jewel and Norfolk Giant were intermediate, Jewel having the fewer secondary buds but rather the more tertiaries. The samples taken were probably too few to detect gradients of bud development along the canes, as reported by both Waldo and Mathers, but there was a suggestion that in Malling Promise and Norfolk Giant the basal primary buds contained fewer flowers and were less differentiated than those at higher levels.

Effects of shortening or removing primary laterals.

It is a common observation that the nodes of raspberry canes do not invariably produce single primary laterals, but that even in "normal" seasons additional laterals may develop, mainly from secondary buds. This is still more marked in years when young primary laterals suffer damage by spring frosts, wind or the larvae of the Raspberry Moth. The variety Lloyd George has a particular reputation for ability to recover from such injury by producing sufficient secondary laterals for a useful, though late, fruit crop.

To gain more information on this subject an experiment on the artificial shortening of primary laterals was carried out in spring 1953, using the varieties mentioned in the previous section. The twelve treatments comprised shortening the laterals by three different amounts (1, removal to the base ; 2, removal of half the lateral ; 3, removal of the tip only) on four successive dates (A—D) spaced at two- to four-weekly intervals between late March and the beginning of June. The actual dates were chosen according to the individual growth of the varieties, but in the A treatments on all four varieties and in the B treatments on Malling Jewel it still proved necessary to postpone some of the cuttings at levels 2 and 3 until the laterals had grown sufficiently for only their end portions to be removed (see Table II). Each treatment was applied to four canes selected at random within single plots of 16–17 stools of each of the four varieties, twelve untreated canes of each variety being recorded as controls. The plots formed a continuous row flanked by other raspberries.

Subsequent records of total lateral formation on the control canes and of the formation of secondary and tertiary laterals on the treated canes showed that the growth produced was reconcilable in all cases with the results of the March bud dissections. In Lloyd George the general result of the treatments was to induce a greatly increased production of secondary laterals and a considerable increase of tertiary laterals, whereas in Malling Promise most of the nodes that showed regeneration—nearly 90 per cent. of the total given treatment B1—formed tertiaries only. The treated nodes of Norfolk Giant produced mainly secondary laterals, with some tertiaries, and those of Malling Jewel hardly any regeneration at all except following the hardest cutting on the first two dates, when moderate numbers of secondaries and tertiaries were formed. Lloyd George clearly showed the most effective

regeneration, followed in order by Norfolk Giant, Malling Promise and Malling Jewel. The tertiary laterals on Malling Promise, though numerous, were in general too weak to provide effective replacement of the primaries.

The same records showed that the harder the primary laterals were cut, irrespective of variety or date, the higher was the percentage of nodes that produced new laterals and that late cutting stimulated least new growth. There was a suggestion that the greatest regeneration followed cutting at the second date, possibly because growth then was more active than when the first treatments were applied.

The fruit yields of the experiment, shown in Table II, reflected the combined influence of the following factors : (i) the yield-reducing effect of the late treatments, which removed the crop of the primary laterals at a time when replacement was no longer possible ; (ii) the tendency of light cutting to depress the formation of new laterals whilst retaining a higher proportion of the yield of the primary lateral ; (iii) inherent varietal differences in ability to regenerate lateral growth.

TABLE II.

Experiment on shortening of primary laterals ; fruit yields in gm. per 100 nodes.

Treatment	Date	Yield			
		Lloyd George	Norfolk Giant	Malling Promise	Malling Jewel
Control		66	67	40	69
A1	27th March–1st April	67	48	12	39
A2	27th March–18th April	61	25	19	22
A3	1st April–29th April	42	17	26	26
B1	10th April–29th April	62	25	18	13
B2	10th April–29th April	52	30	24	17
B3	10th April–4th May	64	19	29	18
C1	24th April–13th May	73	13	14	8
C2	24th April–13th May	45	15	22	13
C3	24th April–13th May	40	22	25	17
D1	28th May–10th June	26	3	2	1
D2	28th May–10th June	29	10	6	2
D3	28th May–10th June	45	21	7	10

This experiment confirmed that Lloyd George could recover from primary lateral injury better than other well-known varieties ; yet most of the treatments depressed its yield. Reductions of crop were greatest, however, in Malling Jewel, followed in order by Malling Promise and Norfolk Giant, both of which were distinctly poorer in recovery than Lloyd George. The results emphasize the special danger of late injury to fruiting laterals. Where these were shortened in late April or early May the loss of crop was generally greater than after the same treatments applied two weeks earlier, and still heavier losses followed the late May–early June treatments.

Some effects of variety and season on the formation of laterals.

Varietal differences in years of average growing conditions.

Following the above work a survey was made in June 1953, and again a year later, of the production of fruiting laterals in ten raspberry varieties in a replicated trial established at Forfar, Angus, since 1947 (Wood and Boase, 1952). Records were taken on three of the six plots of each variety, using ten canes equidistantly spaced along the middle row of each plot. The laterals were counted on all nodes bearing growth, other nodes being ignored. In neither year was the plantation affected by serious spring frosts or other special climatic features, but in both there was some early damage to buds by larvae of the Raspberry Moth.

The results, summarized in Table III, showed that Lloyd George and Malling " M " (of which Lloyd George is the male parent) were outstanding for their number and variety of laterals and especially their production of secondary laterals unaccompanied by primaries. Malling Notable (of the same parentage as " M ") behaved similarly, though rather more of its nodes bore primary laterals only. Secondary laterals were also numerous in Norfolk Giant and Malling Landmark, but were more often accompanied by primaries. Malling Promise, Malling Jewel, Malling Enterprise, Newburgh and St. Walfried showed higher percentages of nodes with primary laterals only. In the last four most of the other laterals present were secondaries, but in 1953 Malling Promise was exceptional for its number of tertiary laterals. In 1954, when these and secondaries were in general fewer, it had primary laterals alone on all recorded nodes.

These results, which were reasonably consistent for the two years and agree with general observation over a longer period, are considered a fairly good indication of the normal behaviour of the varieties, at least in the East of Scotland. The main effect of Raspberry Moth damage, which was fairly extensive in 1954, particularly in the variety Newburgh, was to destroy all growth at some nodes on the lower parts of canes. Such nodes were excluded from the records, but damage confined to primary buds was partly responsible for the high numbers of secondary laterals in Lloyd George and its derivatives in both years.

Differences associated with season and, in particular, the occurrence of die-back.

In spring 1955 the variety Malling Promise at Mylnefield showed an abnormal type of growth in which many nodes, instead of forming primary laterals, produced tertiary laterals either singly or in groups of up to seven (Fig. 3). This occurred mainly towards the tops of the canes and was first seen in early April, before any occurrence of spring frosts of the kind usually damaging to young raspberry laterals but not long after a period of exceptionally hard winter frost in February and early March, when daily grass minimum temperatures of around 0° F. were recorded on several occasions.

In other respects the formation of fruiting laterals on most varieties at Mylnefield that year was fairly normal, but as the season progressed it became evident that serious losses of canes, chiefly of Malling Promise, were occurring further inland, especially, it seemed, in low-lying fields, local hollows and fields exposed to the north or north-east. Many canes died without commencing growth (Fig. 4). Others formed varying numbers of laterals, some or all of which wilted and died during the spring or as the fruit began to ripen. Where any growth was present, tertiary laterals

TABLE III.

Lateral formation at Forfar in 1953 and 1954, on 30 canes of each variety.

Variety	Year	Total cropping nodes*	Percentages of nodes furnished with :							Total laterals	Laterals per node
			P	S	P+S	P+T	T	S+T	P+S+T†		
Lloyd	1953	512	38·7	24·0	30·5	0·2	1·8	4·5	0·4	720	1·41
George ..	1954	435	63·3	19·0	10·7	1·3	2·1	3·4	0	519	1·19
Malling Enterprise	1953	513	99·3	0	0·3	0	0·3	0	0	515	1·00
	1954	392	98·5	0·5	0	0·9	0	0	0	397	1·01
Malling Jewel ..	1953	400	90·5	3·8	3·5	0	0·8	1·2	0·2	428	1·07
	1954	320	96·7	1·6	1·3	0·3	0	0	0	326	1·02
Malling Landmark ..	1953	238	72·3	5·9	20·6	0	0	1·2	0	294	1·24
	1954	226	70·5	9·0	19·6	0	0·8	0	0	271	1·20
Malling "M" ..	1953	580	36·9	34·3	27·4	0	0·2	0·9	0·3	754	1·30
	1954	425	51·9	27·6	17·2	0·2	0·3	2·5	0·2	515	1·21
Malling Notable	1953	632	62·0	20·3	17·2	0	0	0·2	0·3	746	1·18
	1954	521	76·2	15·1	7·9	0	0·7	0	0	566	1·09
Malling Promise ..	1953	367	87·2	3·8	0·8	0·3	5·7	2·2	0	411	1·12
	1954	367	100·0	0	0	0	0	0	0	367	1·00
Newburgh ..	1953	460	94·6	3·5	0·7	0	0·4	0·7	0·2	474	1·03
	1954	330	93·7	4·4	1·0	0·3	0	0·5	0	337	1·02
Norfolk Giant ..	1953	405	66·3	18·0	15·7	0	0	0	0	471	1·16
	1954	322	70·9	11·3	16·7	0	0·7	0·3	0	381	1·18
St. Walfried ..	1953	451	81·8	7·5	10·0	0	0	0·4	0·2	502	1·11
	1954	380	95·5	3·1	0·8	0	0	0·5	0	386	1·02

* Nodes carrying laterals expected to flower and fruit.

† P, S, T ; primary, secondary and tertiary laterals respectively.

could readily be found. Partial or complete failure to produce fruiting laterals was also noted in other varieties, especially Lloyd George, but the damage was less extensive than in Promise and the type of lateral growth present was generally within the normal range. It was interesting that no obvious abnormality was seen at Mylnefield in Malling Exploit, growing alongside Promise, although these two varieties share the same parentage and reach bud-burst at about the same time. Examples of severe die-back in loganberries, resembling that in Malling Promise raspberry, were seen by one of us in Scotland and Worcestershire. At one site in Scotland there was much more damage where the canes had been tied to the wires early than where they had lain under snow during late winter.

Circumstantial evidence strongly suggested that the damage described had been caused by the late winter frosts, especially as the symptoms agreed closely with those of winter injury as described in North America (see later). There also seemed a possibility that the weather of the previous summer and autumn, which had been very wet and dull, had contributed by promoting an immature type of growth unduly liable to frost injury.

In 1956 most Scottish plantations were distinctly improved in appearance. There was again a period of severe late frost in February, but the summer and autumn of 1955 had been unusually sunny and dry and the canes, though somewhat short in growth, had apparently entered the winter well matured. Many plantations seen in both seasons were much better furnished with fruiting laterals in 1956, and growth that year in certain districts, including the Carse of Gowrie, was outstandingly good. There were, however, some exceptional plantations, mainly but not entirely in the Blairgowrie and other inland districts, where failure of second-year canes was as serious as in 1955. In the low-lying field of about 12 acres shown in Fig. 5, practically all the canes died without beginning to form laterals. The pronounced branching of many was caused by frost in early June 1955, during the first year of growth, and most of the branches were thin, possibly as a result of the succeeding drought. There is no satisfactory evidence to explain these failures in 1956, but it is suspected that under certain local conditions the late winter frosts were again damaging. The losses were almost entirely in Malling Promise.

At Mylnefield, where growth in 1956 was good, the formation of fruiting laterals was again recorded in detail. The data for the two seasons, shown in Table IV, were obtained from the same single plots of a variety trial planted in 1952, the unit samples consisting of 30 canes selected evenly from 90 stools. The most striking differences are to be seen in the figures for Malling Promise, although other varieties —especially Lloyd George—also had fewer secondary and tertiary laterals in 1956 and higher percentages of nodes with primary laterals. The records for Malling Exploit indicate that this variety forms secondary laterals more freely than Malling Promise, whilst those for the other varieties are in general harmony with the survey results from Forfar (Table III) and the data from bud dissections.

DISCUSSION.

The present observations show that a more elaborate and varied pattern of flower initiation exists at the nodes of red raspberry canes than is commonly represented by the growth of single fruiting laterals. Varieties differ in the number and position of the inflorescence primordia formed and in the subsequent behaviour of these

TABLE IV.

Lateral formation at Mylnefield in 1955 and 1956, on 30 canes of each variety.

Year	Variety	Total nodes	Total cropping nodes*	Laterals present				Laterals per cropping node	% cropping nodes with P laterals
				P*	S	T	Total		
1955— 9th-10th May	Norfolk Giant ..	671	556	536	39	2	577	1·04	96·4
	Lloyd George ..	686	625	494	197	108	799	1·28	79·0
	Malling Promise ..	668	542	329	15	578	922	1·70	60·7
	Malling Exploit ..	602	506	486	97	13	596	1·18	96·0
	Malling Jewel.. ..	743	604	590	25	4	619	1·02	97·7
	Malling Enterprise ..	679	538	536	1	8	545	1·01	99·6
1956— 29th-31st May	Norfolk Giant ..	649	533	515	44	3	562	1·05	96·6
	Lloyd George ..	764	677	643	160	8	811	1·20	94·8
	Malling Promise ..	647	480	478	1	3	482	1·00	99·6
	Malling Exploit ..	615	474	461	38	9	508	1·07	97·3
	Malling Jewel.. ..	682	523	518	6	1	525	1·00	99·0
	Malling Enterprise ..	653	538	536	1	1	538	1·00	99·6

* As in Table III.

PLATE I

Fig. 1.
Cane nodes of Lloyd George raspberry showing primary and secondary buds.

Fig. 3.
Tertiary laterals on upper portion of a Malling Promise cane in 1955.

Fig. 4.
Failure of fruiting canes of Malling Promise in 1955.

Fig. 5.
Failure of fruiting canes of Malling Promise in 1956.

[*face p. 180*

under variable environmental conditions. These are inherited characters of some economic significance and therefore of concern to the breeder.

The experiment in which primary laterals were artificially shortened gave an indication of how the four varieties could react to similar injury caused naturally. Thus Lloyd George has long been recognized as rather susceptible to frost but able to recover by freely forming new laterals. Malling Promise, at least in Scottish experience, has suffered less from spring frosts than might have been expected of an early variety, but when its primary laterals do become injured the regeneration from the same nodes consists mainly of tertiary laterals, generally too weak to provide adequate replacement. The quality of such laterals, however, evidently can vary with their time of formation, for many that were produced early by this variety in 1955 (Table IV) grew fairly strongly and contributed to the crop. Another feature of Malling Promise, it may be added, is that a proportion of the primary buds may be delayed in growth, and form productive laterals after earlier ones have been frosted (Wood, 1950). Malling Jewel, which recovered poorly in the experiment, has in practice proved somewhat frost resistant and is liked for situations of moderate risk ; but it would probably suffer seriously in yield if its primary buds or laterals were damaged through any other cause. The late-flowering Norfolk Giant also suffers comparatively little frost injury but forms secondary laterals fairly frequently even without damage to the primaries.

The die-back of fruiting canes of Malling Promise in 1955 was much more extensive than the cane losses—some due to known causes, others unexplained—that occur in Scottish plantations in average seasons. In the worst-affected places there was an almost complete loss of crop. Attempts to identify a pathogen as the main cause were unsuccessful or inconclusive and were complicated by the undoubted presence of certain common fungal infections, especially Spur Blight (*Didymella applanata*) and Grey Mould (*Botrytis cinerea*), which had apparently been favoured by the previous year's weather and had contributed to the total cane mortality. Winter frost injury, which the writers suspect to have been mainly responsible, has received more investigation in cane fruits in North America than in this country, although as long ago as 1928 it was observed by Harris (1931) in blackberries and raspberries in Kent. The damage in North America may take place at various times in the winter (Bradford, 1922), but recent studies by Brierley (1945), Brierley and Landon (1946, 1954), Brierley, Landon and Stadtherr (1952) and others, working mainly in Minnesota, have shown that it commonly occurs when winter temperatures fluctuate from cold to warm and again to cold. The condition of true dormancy of the canes in late autumn is first " broken " by a period of cold weather, after which a short period with air temperatures slightly above freezing point can cause loss of resistance to further cold. Canes thus dehardened may reharden to some extent if temperatures remain below the level for bud activity (Brierley and Landon, 1954) but, should bud growth commence and be followed by a return of cold weather, injury to the buds and canes is likely to occur. The symptoms of such injury, both as described from the field by the above workers and as induced by them experimentally, closely resemble what was seen in this area in 1955. Berkeley and Chamberlain (1944), describing winter injury of raspberries in Canada, noted the several forms it could take and varietal differences in susceptibility, and stressed the danger of autumn immaturity of canes, a factor considered of less or variable importance by some U.S.A. investigators (Shoemaker, 1948). The different

autumn conditions that preceded the 1955 and 1956 seasons in Scotland have already been mentioned, but the occurrence of the main frosts of each winter as late as February raises the question, in the light of the American work, of whether temperature variations during the earlier winter months were critically different in the two years. Meteorological records at Mylnefield suggest that this may have been so. Prior to the frosts of February 1955 there were ten days of fairly hard frost in mid-January, with minimum air temperatures between 26° and 10° F., followed by ten days of warmer weather on five of which the daily minima exceeded 40° F. The temperatures a year later were more uniform, with no sustained frost before February.

No proof has yet been obtained that the damage under discussion was caused by frost, although the circumstantial evidence supports that view. Further work on the problem is contemplated. A similar development of die-back, also inadequately explained at the time, occurred in the East of Scotland in the variety Norfolk Giant (then in wider use) following the severe late winter in 1947. It appears that some, at least, of the raspberries now commercially important are liable to occasional serious damage of this kind and that the matter may be one to consider in the selection of new varieties.

SUMMARY.

1. Certain varieties of red raspberry generally bear two distinct buds (here termed primary and secondary) at each cane node. In the scale axils of these are smaller buds (termed tertiary). Inflorescence primordia may be found from late September onwards in buds of all three types, the largest and earliest-formed being on the main axes of primary buds.

2. All types of bud can produce fruiting laterals ; but field surveys in two seasons of fairly average climatic conditions (1953 and 1954) showed that, whilst most of the laterals in ten varieties were formed from primary buds, there were marked varietal differences in the extent to which secondary and tertiary buds produced laterals.

3. An experiment involving the shortening of primary laterals in spring showed varietal differences in the amount of replacement growth formed from secondary and tertiary buds and in the effects of the treatments on fruit yield.

4. Canes of the variety Malling Promise in 1955 suffered severe damage (" die-back ") considered to have been caused by the weather of the preceding autumn–winter period. Where complete cane death did not occur there was more injury to individual buds in this variety than in others. The problem of winter injury is discussed.

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THE EFFECT OF REMOVING APICAL SECTIONS OF THE STEM ON THE FLOWERING BEHAVIOUR OF NON-VERNALIZED CHRYSANTHEMUMS

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It has been shown (Schwabe, 1950) that plants of *Chrysanthemum morifolium* var. Sunbeam, raised from basal cuttings (i.e. from shoots arising below ground level) taken from parent plants grown and flowered at high temperatures, require a period of low temperature or vernalization in order that normal stem elongation and rapid flowering may occur. Without such treatment, plants grown in high temperature conditions (> 60° F.) fail to elongate normally (i.e. they produce a rosetted type of growth) and are considerably delayed in flowering.

During the course of growing a batch of non-vernalized plants of Sunbeam and President in short photoperiods, it was observed that on a few plants a lateral shoot elongated and flowered some distance behind the growing point, which continued to grow vegetatively. Flowering laterals in the presence of a vegetative main apex were also observed by Schwabe in incompletely vernalized plants of Sunbeam. The experiments described here were undertaken to investigate the behaviour of lateral shoots which develop on non-vernalized plants when the growing point and part of the stem are removed.

Reports in the literature indicate that in several unrelated species removal of the apical section of the stem results in accelerated flowering, or in the flowering of lateral shoots which would otherwise have been inhibited in growth. Wareing (1953) reported that male cones of *Pinus sylvestris* could be produced prematurely on "juvenile" trees by removal of the terminal bud. Kikuyu grass flowers only when the herbage is grazed or cut (Edwards, 1937; Parker, 1941). Carr and Eng Kok Ng (1956) have shown that the suppressed lateral buds are vegetative but begin to initiate spikelets immediately the stolon tip is removed.

The results published in this paper show that under certain conditions flowering of non-vernalized plants of *C. morifolium* can also be markedly accelerated by removing apical sections of the stem. A preliminary report was published in Nature (Vince and Mason, 1954).

Methods.

Non-vernalized plants for all experiments were raised from basal cuttings taken from plants grown and flowered at temperatures above 60° F. and then cut to ground level. Cuttings were rooted and subsequently grown in a thermostatically controlled glasshouse at temperatures of above 60° F., except in Exp. 4 where periods of low

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temperature at 40° F. were given as stated in the text. Short-day treatment consisted of eight hours of natural daylight, except in Exp. 1 where this was supplemented by 2 hours of low-intensity artificial light from daylight fluorescent tubes and 15-watt tungsten-filament lamps to give a total photoperiod of 10 hours.

RESULTS.

Exp. 1. Effect of cutting back plants at three different levels.

Non-vernalized plants of Sunbeam, from cuttings taken on 30th December 1953, were grown in natural daylight until 15th June 1954. On this date the plants, which had approximately 50 expanded leaves, were cut back to 25, 35 or 45 leaves or left intact and were placed immediately in short-day (10-hour) conditions. The number of replicates was four. The laterals, which developed when the apical sections were removed, elongated and rapidly produced macroscopically visible flower buds. The main axes of the intact plants continued to show rosetted and diageotropic growth, and only flowered after some delay. In most of the plants two or three lateral shoots developed as a result of removing the apex ; each shoot was recorded but only the values for the distal laterals are given, since all responded in the same way.

The acceleration of flowering is shown by the decreased number of weeks (from date of commencement of the short-day treatment) required for budding of the distal lateral of cut-back plants as compared with the main axis of intact plants ; also by the decreased number of leaves on the laterals of cut-back plants as compared with the approximate number of leaves laid down on the main axis of intact plants from commencement of the short-day treatment to flowering (Table I). The increased internode length on the lateral shoots is also apparent.

The results for the three levels of cutting back did not differ significantly from one another at the 5 per cent. level of probability, but the trend of the figures is for greater acceleration of flowering and an increase in internode length when a smaller number of leaves is removed.

TABLE I.

Effect of cutting back on flowering and internode elongation in non-vernalized plants, var. Sunbeam.

	Intact plants*	Cut back* to leaf number			Sig. diff. between means, P=0·05
		25	35	45	
Days to visible bud from commencement of short days	84	57	49	43	18·2
Leaf number to bud from commencement of short days. Total leaf number in brackets ..	36·0 (86·0)	15·7 (40·7)	15·7 (50·7)	13·7 (58·7)	10·6
Mean internode length (cm.)	0·60	1·13	1·99	1·66	0·52

* Figures for intact plants refer to the main axis, those for cut-back plants to the distal lateral only.

Exp. 2. Effect of application of β-indolyl acetic acid (IAA) and 2: 3: 5 tri-iodo benzoic acid (TIBA) coupled with removal of apical sections of the stem.

Non-vernalized plants of Sunbeam, raised from cuttings taken on 11th December 1953, were grown in natural day length conditions. Half the number of plants were cut back to 35 leaves on 18th June, and spray treatments and short days commenced four weeks later. Sprays of TIBA or IAA (50 p.p.m. in aqueous solution) were applied twice weekly to the leaves ; the control plants were not sprayed. The number of replicates was seven.

The effect of cutting back was the same as in the previous experiment ; Table II shows that flowering was accelerated (earlier budding and decreased leaf number) and internode length increased on the laterals as compared with the main axis. All laterals were recorded but values for distal laterals only are given.

The spray treatments did not affect flowering of either intact or decapitated plants. In some plants internode length was greater with IAA sprays, or less with TIBA sprays, than in the controls, but the response was variable and the means did not differ significantly.

TABLE II.

Effect of application of β-indolyl acetic acid (IAA) and 2 : 3 : 5 tri-iodo benzoic acid (TIBA) coupled with cutting back on non-vernalized plants, var. Sunbeam.

	Intact plants			Cut back to 35 leaves			Sig. diff. between means, P=0·05
	Control	TIBA	IAA	Control	TIBA	IAA	
Days to visible bud from commencement of short days	124	138 124·6*	112	40	36 44·1*	56	N.S. 42·7
Leaf number† to bud ..	104·4	104·1 103·5*	102·1	55·0	51·9 55·5*	59·7	N.S. 14·6
Mean internode length (cm.)	0·52	0·40 0·50*	0·58	1·41	1·50 1·46*	1·46	N.S. 0·51

* Mean values for all spray treatments.
† Leaf number of main stem (35) plus leaf number on lateral for cut-back plants.

Exp. 3. Effect of cutting back on the variety President.

The variety President, which shows extreme rosetting and is very delayed in flowering when not vernalized (Vince, 1955), was also subjected to the treatments described in Exp. 1 and Exp. 2. In the first of these the lateral shoots of cut-back plants began to elongate, but in all except two plants (10·5 per cent. of the total) they re-rosetted and remained vegetative. In the second experiment approximately 50 per cent. of the cut-back plants flowered :

	Intact plants	Decapitated plants
No. of plants flowering	0 ..	10
No. of plants vegetative	19	11

$\chi^2=9{\cdot}66$ (P=0·01).

As in the experiments with Sunbeam, the spray treatments did not affect the response.

Thus, decapitation followed immediately by short days as in Exp. 1 did not affect the flowering of President but, when four weeks of long photoperiods (*ca.* 18 hours) followed the cutting back, the laterals elongated and some of them afterwards flowered when placed in short days. The effect of cutting back may not be a direct one since in President some intact non-vernalized plants will flower when a period of continuous light is followed by short days (Mason, 1956). In order to be effective the continuous light treatment must be given as early in the life of the plant as possible ; if short photoperiods precede the continuous light, the response is decreased. Cutting back may, therefore, have resulted in the development of younger shoots able to respond to the long day conditions. It should be noted that in Sunbeam a period of long days cannot take the place of low temperature ; this has been reported by Schwabe (1952) and confirmed in this laboratory. In Sunbeam a period of long days following the decapitation did not affect the flowering response of the laterals.

Exp. 4. Effect of partial chilling on the response to removal of apical sections of the stem.

Schwabe (1954) has criticized the results of Exp. 1 on the grounds that the production of flowering laterals in the presence of a vegetative main apex is indicative of a partly vernalized, or incompletely de-vernalized, condition and has suggested that the results were due solely to partial chilling. It is the contention of the authors that the abnormal flowering behaviour observed, viz. the production of axillary flowering shoots while the terminal growing point remains vegetative in this normally determinate plant, occurs in the wholly non-vernalized state. However, in order to investigate the possibility that a short period of chilling might affect the response, plants were either cut back or left intact after receiving varying periods of low temperature.

Non-vernalized plants of Sunbeam, from cuttings taken on 12th October 1954, were grown in natural days until 5th April 1955 (maximum day length *ca.* 14 hours)

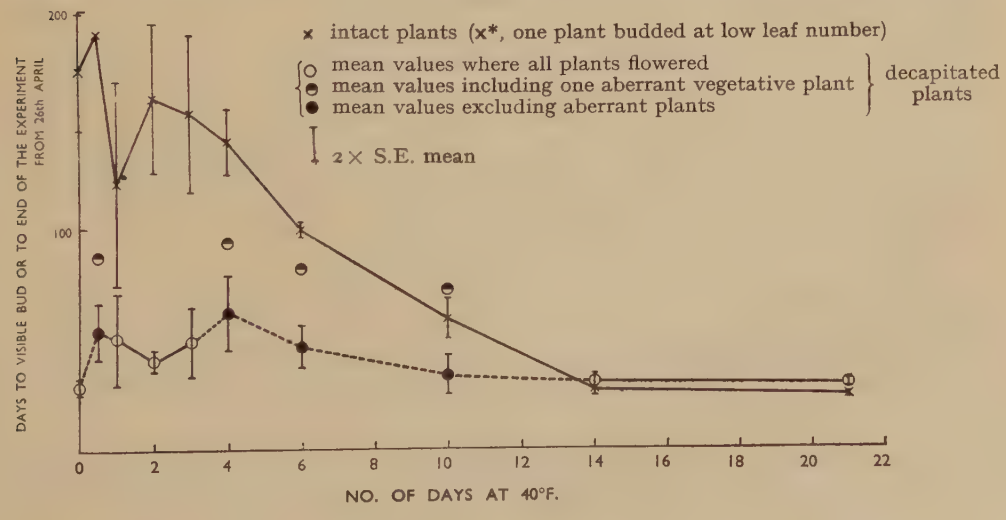

Fig. 1.

Effect of low temperature on response to decapitation, var Sunbeam; mean number of days until bud formation.

when the plants were transferred to short days. Ten periods of low temperature (40° F. in short days) were given, varying in length from 0 to 21 days and all terminating on 26th April ; the number of replicates was eight. On 26th April an apical stem section with ten expanded leaves was removed from each of four plants in each temperature treatment ; all plants were then transferred to short photoperiods at temperatures of above 60° F. The number of expanded leaves on 26th April ranged from 35 to 49.

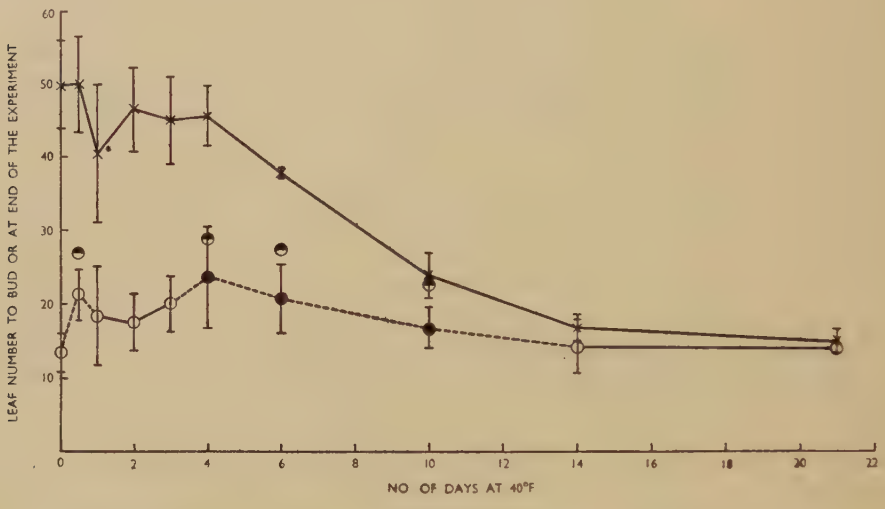

Fig. 2.

Key as in Fig. 1.

Effect of low temperature on response to decapitation, var. Sunbeam ; mean number of leaves formed before budding.

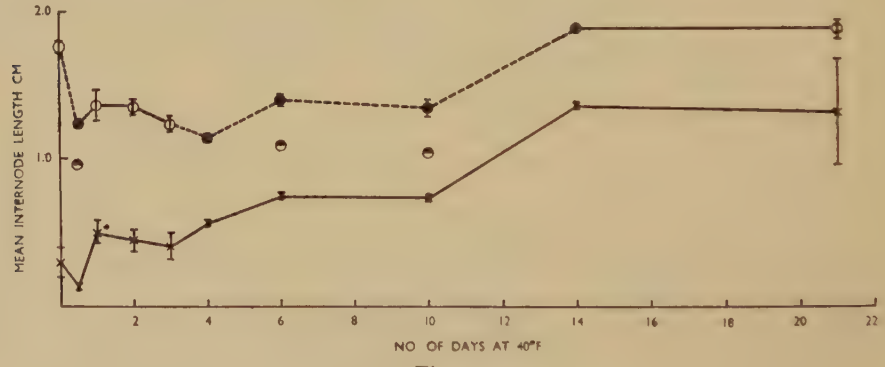

Fig. 3.

Key as in Fig. 1.

Effect of low temperature on response to decapitation, var. Sunbeam ; mean internode length.

Thirty-six of the decapitated plants produced laterals which elongated and flowered rapidly. The laterals on the remaining four plants (in four temperature

treatments) elongated, but later re-rosetted and were still vegetative at the end of the experiment (27 weeks from the end of the chilling treatment). The mean values (with and without these plants) for number of days to bud, leaf number to bud and internode length are given in Figs. 1, 2 and 3 respectively. In cut-back plants the time of budding was not affected by the temperature treatment, but in intact plants flowering was considerably delayed when less than 14 days of cold was given. Twelve of the plants which received 3 days or less of low temperature remained vegetative. No flowering laterals were observed on any of the intact plants ; incomplete chilling did not, therefore, bring about this type of flowering behaviour.

Partial chilling resulted in a somewhat variable flowering behaviour in both intact and decapitated plants and Bartlett's test showed that the data for days to bud are not homogeneous. An analysis after transformation to reciprocals showed that the effect of decapitation in decreasing the number of days to bud was highly significant ($P < 0{\cdot}001$). Comparison of the temperature treatments showed that cutting back resulted in a significant ($P < 0{\cdot}05$) delay in the budding of completely vernalized plants (21 days cold). When 14 days cold was given, intact and decapitated plants budded at the same time. In all treatments with less than 14 days cold, budding was significantly accelerated by cutting back.

Fig. 3 shows that the mean internode lengths on the part of the main stem which developed after chilling decreased as the duration of the chilling treatment was decreased. The mean internode lengths on the laterals were always greater than those on the main axis.

Exp. 5. Effect of age of the plant on the response to cutting back.

Experiments 1, 2 and 4 showed a marked acceleration of flowering in non-vernalized plants in response to cutting back but in some subsequent experiments, although the laterals elongated initially, they later re-rosetted and remained vegetative. The only consistent difference between successful experiments and those in which the laterals failed to flower appeared to be the age of the plants when decapitated. This was investigated in the following experiment.

Non-vernalized plants of Sunbeam, from cuttings taken on 28th October 1955 and rooted in short photoperiods, were potted on 11th November and grown on in short-day conditions. Four weeks after the date of potting, an apical stem section with five expanded leaves was removed from each of five plants and at two-week intervals further groups of five plants were similarly decapitated. Only the distal lateral was allowed to develop on each plant. The experiment was discontinued on 28th August, 40 days after the final decapitation.

The results are given in Table III, which presents the flowering response to decapitation in terms of days to bud from an arbitrary date (1st June), days to bud from the decapitation date, and the percentage of plants flowering in each treatment. All control (intact) plants were rosetted and vegetative when the experiment was terminated. Lateral shoots developing on plants decapitated before 20 weeks rosetted and remained vegetative at the end of the experiment. When plants of an increasingly greater age were cut back, an increasing percentage of the laterals elongated and flowered, and in the last four treatments 18 of the 20 plants flowered rapidly. When plants were cut back between 20 and 30 weeks, the laterals either responded fairly rapidly or rosetted and remained vegetative, and this variable response is reflected by the large standard errors in these treatments.

TABLE III.

Effect of age of the plant on the response to cutting back, var. Sunbeam.

Age in weeks at decapitation	Days to visible bud from 1st June	S.E. (±) of mean	Days to visible bud from date on which plants were cut back	S.E. (±) of mean	Percentage of plants flowering
4	90*		262*		0
6	90*		248*		0
8	90*		234*		0
10	90*		220*		0
12	90*		206*		0
14	90*		192*		0
16	90*		178*		0
18	90*		164*		0
20	48	39·9	109	38·8	60
22	78	27·3	124	26·4	20
24	76	30·4	109	29·5	20
26	70	30·3	89	29·3	40
28	50	38·9	56	35·8	60
30	47	27·6	38	26·7	80
32	53	6·2	31	6·2	100
34	64	14·7	27	13·8	80
36	71	0·0	21	0·0	100
Intact plants ..	90*				0

* All plants vegetative at the end of the experiment.

χ^2 for difference between number of plants flowering in age groups 0–18 weeks and 20–36 weeks = 114·0 ($P < 0·001$).

When only reproductive laterals are considered, the number of days to bud and the leaf number on the laterals decreased as the plants were cut back at a later and later date (Table IV). The low leaf numbers on the lateral shoots in treatments 16 and 17 suggest that initiation had already occurred before cutting back. No

TABLE IV.

Effect of age of the plant on the response to cutting back—flowering laterals only, var. Sunbeam.

Treatment number	Age in weeks at decapitation	Days to visible bud from date on which plants were cut back	S.E.± of mean	Number of leaves on lateral	S.E.± of mean
9	20	82	15·6	31	5·1
10	22	77	*	24	*
11	24	56	*	27	*
12	26	59	24·7	23	5·0
13	28	30	10·2	17	3·5
14	30	21	15·1	14	7·9
15	32	31	6·3	17	4·0
16	34	21	0·0	5	3·1
17	36	21	0·0	4	0·8

* Only one plant flowered.

lateral shoots, either flowering or vegetative, developed on any of the intact plants during the course of the experiment.

The results of the experiment suggest, therefore, that non-vernalized plants of Sunbeam cannot respond to decapitation until they reach a certain age ; plants showed some degree of flowering after 20 weeks and nearly 100 per cent. response after 28 weeks in short photoperiods. The response may well be related to plant size rather than to plant age, since in Experiments 1, 2 and 4, which gave nearly 100 per cent. flowering response, the comparable ages (i.e. calculated from 14 days after the date of insertion of the cuttings) were 22, 25 and 26 weeks respectively.

DISCUSSION.

Non-vernalized plants of *C. morifolium* var. Sunbeam are able to initiate inflorescence primordia at lateral meristems under conditions where the apical meristem continues to grow vegetatively for some time. The experiments described do not distinguish between the initiation of inflorescence primordia before or after decapitation. In the former case, extension growth of the reproductive laterals would normally be suppressed by apical dominance until the apex had been removed. The number of leaf initials within the axillary bud is usually not more than five and, since most of the laterals flowered with more than ten leaves, it seems likely that initiation occurred subsequently to decapitation in the majority of cases. Probable exceptions are the final treatments (Nos. 16 and 17 of Table IV) of Exp. 5,where the mean leaf numbers were five and four. Consideration of the leaf numbers on the flowering laterals, of the response to age in Exp. 5 and of the response to the degree of cutting back in Exp. 1, suggests that : (i) after a certain age or size, inflorescence initiation in response to short photoperiods can occur at all lateral meristems (at least down to the 25th node from the base) when the apical portion of the stem is removed and (ii) as the plants are grown on in short photoperiods to a greater age, inflorescence initiation occurs at the upper axillary meristems without decapitation. In the experiments described, the plants were grown for a greater part of the time (Exp. 1 and Exp. 2) or throughout (Exp. 4 and Exp. 5) in short-day conditions.

An hypothesis correlating these observed facts may be outlined as follows. In plants which have been adequately chilled short photoperiods initiate a set of reactions which result in flowering, whereas in plants which have not been chilled the same conditions bring about the suppression of internode elongation and the plants fail to flower. It is suggested, therefore, that in non-chilled plants the reaction sequence is shifted towards the production of a substance or complex " I " which inhibits shoot extension, rather than to the production of a substance or complex " F " which initiates flowering. Failure to flower in a non-chilled plant results, therefore, rather from a low rate of F production than from the presence of a specific inhibitor of flowering. Since these reactions occur mainly in short photoperiods, normal shoot extension occurs in non-chilled plants in long days. Experiments with the variety President (Mason, 1956) have shown that marked shoot extension occurs only when the long-day treatment commences early in the life of the plant ; if transfer is delayed until after eight weeks of growth in short days, subsequent long photoperiods are relatively ineffective in causing elongation unless the apical part of the stem is removed. These results with President suggest that long photoperiods prevent the formation of the inhibiting complex I but do not destroy or inactivate

it once it has been built up in short days ; the inhibiting complex apparently remains concentrated in the growing region of the stem.

The effect of cutting back on the variety Sunbeam can be accounted for in the following way. Since this variety eventually flowers in response to continuous short days in the absence of chilling, some flower-promoting substance must build up slowly ; initiation is assumed to occur when the F/I ratio reaches a certain value. The effect of decapitation is to remove most of the inhibitor, which is localized in the growing region. Decapitation of young plants normally results in a certain amount of extension growth due to a lower initial I concentration in the lateral buds, but internode elongation is rapidly suppressed, presumably as the inhibitor concentration builds up in the lateral apices as they become actively meristematic. F, which is slowly accumulated at the growing point, unlike I, is translocated basipetally and the F/I ratio is consequently higher in the axillary buds than at the apex ; after a sufficient number of short photoperiods, removal of the apical stem section lowers the inhibitor level sufficiently to bring about flowering in response to the concentration of F already present in the lateral buds, before the inhibitor level builds up as the meristems become active. Later the F/I ratio builds up to a level at which inflorescence initiation occurs in the upper axillary meristems without decapitation. Finally the F/I ratio reaches the flowering level at the apex.

There is evidence from other experiments to suggest that a supply of F from a source external to the bud concerned can initiate flowering in a shoot which would normally require chilling if detached from the F-supplying region. Shoots developing near the base of a flowering stem normally require chilling before they can flower, but if they remain attached to the flowering stem for a long period (i.e. until after the inflorescence has died) several of these shoots will flower. This has also been observed by Schwabe (1955).

The hypothesis must be considered as very tentative in the absence of the identification of either of the postulated substances. In the theory outlined, no consideration has been given to the rôle of the auxin level *per se* in the plant, but its possible effect should not be overlooked ; some evidence was obtained in Exp. 2 that added IAA could bring about some elongation in non-vernalized shoots, whereas TIBA decreased it.

Since a balance of substances is assumed, the variable response in Exp. 5 to cutting back between the ages of 20 and 30 weeks can be accounted for. It may also be noted that, since the inhibiting complex apparently remains localized in the apical region, no transfer from a non-vernalized plant grafted to a vernalized plant would be expected (see Schwabe, 1954).

The hypothesis may be summarized as follows : (i) in non-vernalized plants in short days a substance which inhibits elongation is produced and remains concentrated in the growing region, (ii) a flower-promoting complex is produced slowly at the apex and is translocated basipetally and (iii) inflorescence initiation can occur when the F/I ratio reaches a certain level.

SUMMARY.

Under certain conditions the flowering of non-vernalized plants of *C. morifolium* var. Sunbeam was markedly accelerated by removing an apical section of the stem. The laterals which developed as a result of decapitation elongated normally and

flowered rapidly in short photoperiods, while the apices of the control (intact) plants continued to show rosetted, diageotropic growth, and terminal inflorescences developed only after considerable delay. Flowering in response to decapitation occurred in wholly non-vernalized plants and was not increased by partial chilling ; in fully vernalized plants decapitation delayed flowering.

This response to decapitation in non-vernalized plants occurred only when they had attained a certain age ; the lateral shoots remained vegetative when plants were cut back less than 20 weeks from the date of potting. Maximum response occurred when plants were cut back after more than 28 weeks of growth in short photoperiods. The response may be related to plant size rather than to plant age since, in three other experiments which gave nearly 100 per cent. flowering after cutting back, the plants were 22 to 26 weeks old.

The flowering of laterals or of intact plants was not affected by the application of sprays of β-indolyl acetic acid or 2 : 3 : 5 tri-iodo benzoic acid ; the mean internode length was slightly greater in the former and smaller in the latter treatment as compared with the values for non-sprayed plants, but the differences were not significant at the 5 per cent. level of probability.

In Sunbeam the flowering behaviour of laterals was not affected when a four-week period of long days followed the decapitation treatment before the transfer to short days. In President only a small number of laterals flowered when decapitation was immediately followed by short photoperiods but, when a four-week period of long days followed decapitation, about half of the laterals subsequently flowered in short days.

A possible explanation of the behaviour of non-vernalized Sunbeam plants in these experiments is suggested.

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THE DEVELOPMENT OF ADVENTITIOUS ROOTS ON HARDWOOD CUTTINGS OF GOOSEBERRIES

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DURING investigations of the external factors influencing the rooting of gooseberry cuttings (5), observations were also made on the origin and development of roots in hardwood cuttings and are reported in this paper.

Rooting in many species normally propagated by cuttings has already been investigated by other workers. Although adventitious roots usually develop in the vicinity of differentiating vascular tissue it appears that, from one species to another, various types of tissue can give rise to roots at predetermined points on the stem. The importance of basal callus for the production of wound roots (i.e. those occurring at or near the basal cut) also varies according to the species.

Some species of Ribes (e.g. black currant) possess pre-formed root initials lying in the cambial region opposite an unusually wide medullary ray (10). These consist of a group of meristematic cells that give rise to roots on planting in suitable conditions. The existence of these initials on unplanted black currant shoots has also been confirmed in the present work (Fig. 1) but no such root initials have yet been traced in unplanted gooseberry shoots. When roots arise on the stem after insertion in the soil without the occurrence of pre-formed initials, various tissues have been reported to be concerned with root formation, viz. the vascular cambium (4), the secondary phloem parenchyma (2) and the parenchyma in the bud gap (11).

Whether callus formation on the basal wound is necessary in the rooting of cuttings also depends on the species. Knight (3) investigated the rooting of hardwood cuttings of various varieties of fruit tree rootstocks and stressed the importance of callusing soon after planting if the cutting was to survive and form roots, which in most cases appeared first *through* the basal callus. Failure to form callus in the varieties investigated resulted in death of the cutting which rotted from the base upwards. Callusing in vine (9), though independent of rooting, always preceded it, the basal wound roots arising just *above* the callus and not through it. In apple and willow, callusing was also found to be independent of rooting (8).

The actual tissue from which the callus arises varies according to the species (6). The pith, medullary rays, cortex (1), phellogen (4) and most frequently the vascular cambium (3) have been reported as tissues from which the basal callus may arise.

Material.

Three hundred cuttings of the gooseberry variety Keepsake were planted at the end of October after having been prepared in the normal manner with all buds removed except for four at the top of the cutting. Sample cuttings were lifted daily at first, and later at intervals of 1–3 weeks throughout the months following planting. The samples were washed free from soil and the main features in the development of roots were observed. A selection of material fixed in formalin-acetic-alcohol was preserved for sectioning.

External features of rooting.

Changes in the basal wound.

Cuttings lifted one day after planting showed a downward swelling of the pith which had previously receded owing to differential tension on cutting the original shoot. This swelling increased during the first eight days after planting but, as no cell division was apparent during this period, the swelling was probably due to increased turgor of the pith cells relative to that of the other tissues.

Callus was first observed as a narrow ring in the region between the wood and the bark on cuttings lifted ten days after planting. A radial expansion of the lowest 2–3 mm. of the cutting indicated internal upward development of the callus also. Subsequent samples showed that callus continued to be produced throughout the winter and its production did not cease at the onset of cold weather.

During the stage between planting and bud-burst the cuttings with the largest amount of callus at the base also had the largest number of roots both on the basal region and on the stem above. As the growing season advanced, this association between callus formation and rooting disappeared and basal roots emerged on cuttings which had no visible callus at the base. Where no basal roots occurred on non-callused cuttings, the latter often survived after dying back from the base to the first node carrying a root.

No callus developed on the apical cut; this was gradually covered by the thickening of the shoots which arose near it.

Rooting.

Basal wound roots did not emerge through the callus ring beneath the cutting but through the bark and callus a few millimetres above the basal cut, and also in the region above the callus. These did not appear to arise in any definite arrangement though later anatomical studies showed that they always originated opposite xylem rays.

In addition to the basal roots, others emerged from the stem, singly at first, in definite positions above each bud scar.

The illustration of a cutting lifted five months after planting (Fig. 2) and at early blossom stage shows roots arising just above the bud scars. The tissues of the outer bark are ruptured by the emergence of the root and, although the wound resulting from removal of the bud is in such close proximity, this is not used as a means of exit by the developing root. Roots produced at later dates occurred adjacent to and immediately above the first formed ones, forming vertical tiers of three or four roots. Later still, roots were seen to appear occasionally at definite positions corresponding with the axillary bud gaps on either side of the bud scars, but this was not so general.

About seven months from planting, branching of the roots occurred and considerable thickening of the original roots began to take place so that a fully developed root system was present nine months from planting.

Anatomical aspects of root and callus formation.

Longitudinal and transverse sections of unplanted and planted shoots were prepared by hand and with a sledge microtome. Sections were stained in safranin-light-green in cellosolve for lignified and unlignified structures, in Sudan III for suberin, and in Delafield's haematoxylin for meristematic tissues.

PLATE I

Fig. 2.

Emergence of roots on gooseberry cutting at predetermined positions above the node; five months after planting.

Fig. 1.

Black currant root initial in unplanted cutting (T.S.).

Notation used in Plates I-III:

x, xylem in cutting; x_1, xylem developed in callus; x_2, xylem developed in pith; ca, cambium; co, cork; p, phloem; pi, pith; ph, phellogen.

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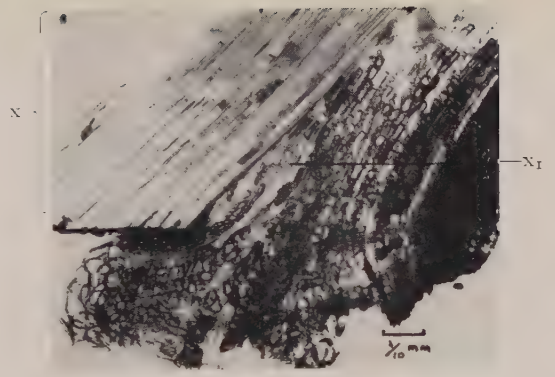


FIG. 3.

L.S. of part of cutting base showing callus development in cambial area five weeks after planting. Xylem elements have started to form in the callus.

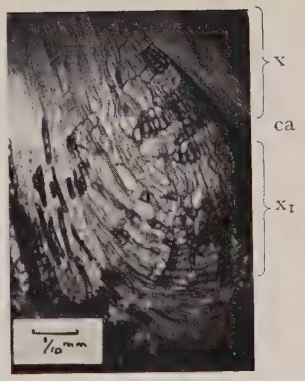


FIG. 4.

L.S. of part of cutting base showing xylem elements developed in callus; eight weeks after planting.

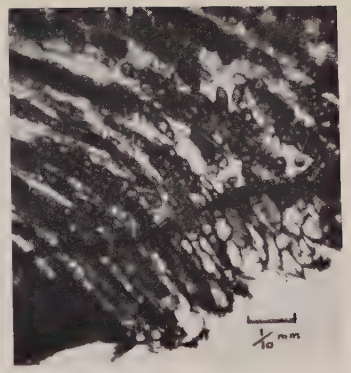


FIG. 5.

L.S. of part of cutting base showing protective layer of cork cells in cortex; five weeks after planting.

PLATE II

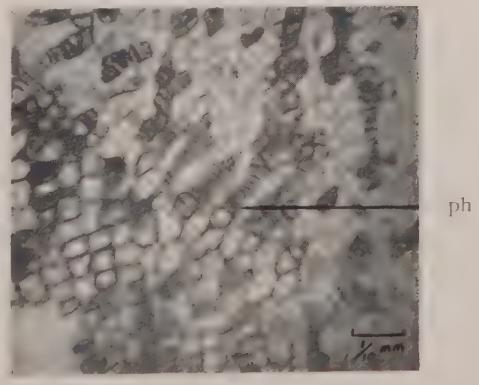
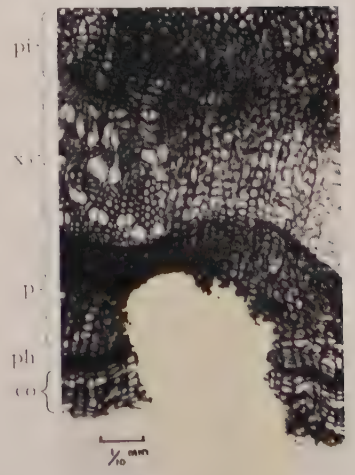


FIG. 6.

L.S. of pith at base of cutting showing layer of phellogen; three weeks after planting

FIG. 7.

L.S. of part of cutting base showing xylem elements beginning to form in the pith.



I

L.S. of base ...h on rooted cutting ...onths from planting, ...g xylem, cambium, ...l and cork lay

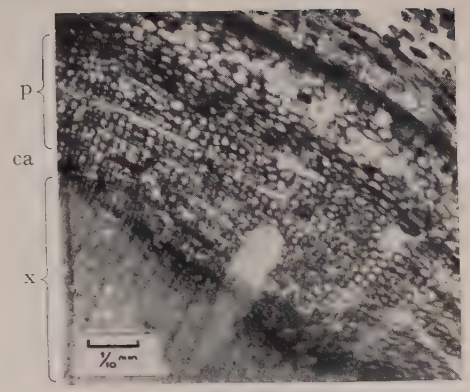


FIG. 9.

T.S. of cutting base showing area of lightly staining cells occurring in the phloem opposite a wide xylem ray, adjacent to which wound roots develop.

FIG. 10.

T.S. of cutting base showing peripheral area of root-forming region becoming meristematic.

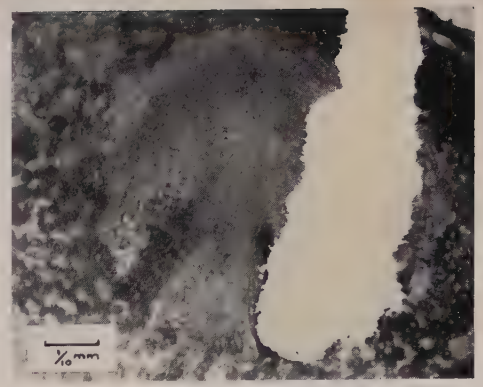


FIG. 11.

T.S. of cutting base showing basal root differentiating into three histogens before emergence.

PLATE III

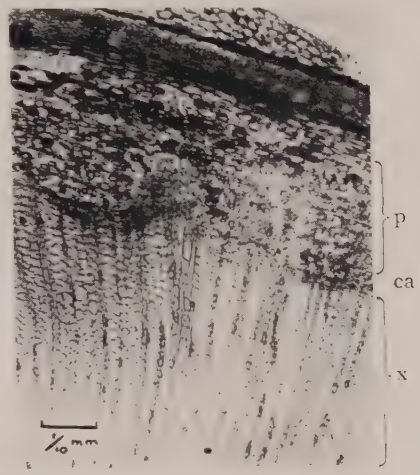


FIG. 12.

T.S. of unplanted cutting in region of bud gap from which nodal roots arise.

FIG. 13.

T.S. of planted cutting showing cells in bud gap dividing to form root primordium.

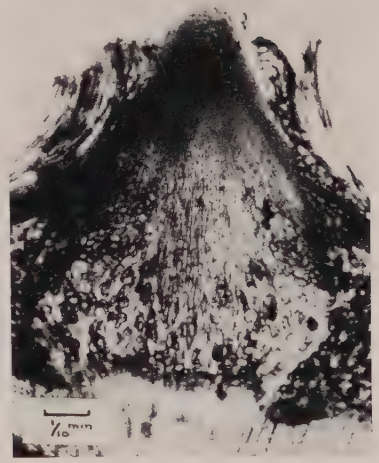


FIG. 14.

T.S. of planted cutting showing emergence of root.

Callus and root formation at base of cutting.

By the third day after planting, the phellogen had cut off cells at the base of the cutting across the bark area to form a protective cork layer. On the eighth day wound gum, similar to that described by Swarbrick (7), was evident blocking one or two of the vessels near the base of the cutting. Seventeen days after planting, the wound gum had formed a definite layer across the base of the xylem approximately 1–2 mm. from the basal cut.

First signs of cell division occurred on the tenth day in the cambial region at the base of the cutting and marked the first stages in the formation of the callus ring. Some of the samples lifted at this stage had failed to form a protective cork layer on the bark edge, in consequence of which the lower cells died back ; on these samples cambial activity commenced further up the stem to form a proliferation of parenchyma near the cambial area above the dead portion of bark.

Two weeks after planting, the cells at the pith margins at the base of the cutting had become meristematic and formed a proliferation of tissue, the outer cells of which became suberized. Also at this time suberin was laid down in a layer of cells across the base of the pith upwards and about five cells deep, but no phellogen was apparent. After three weeks cells adjacent to this layer became meristematic and formed a phellogen between the living pith cells above and the dead and dying cells below (Fig. 6).

On cuttings which produced callus this continued to increase in amount, cutting off cells downwardly and inwardly, and gradually extended across the base of the cutting (Fig. 3). Pro-vascular elements with scalariform thickening developed in the callus outwards from the cambial cells and extended upwards (Fig. 4). By this time the layer of suberized cells cut off previously in the cork layer extended over the whole of the cortex and callus except at the inner edge of the latter (Fig. 5). The callus margins continued to grow downwards and inwards, and the inner areas of callus differentiated into xylem to the outside. The pith margins grew downwards and outwards to a lesser degree and cut off parenchyma and wood elements which finally formed a complete protective layer across the base of the pith 10 months from planting (Figs. 7 and 8).

Wound roots which arose in this region originated in the callus (when present) at the edge of groups of thin-walled, lightly-staining parenchymatous cells which occurred near the vascular cambium on the inner edge of the phloem where the medullary rays enter the phloem (Figs. 9, 10 and 11).

Formation of nodal roots.

Nodal roots occurred only in the region of the bud gap and occasionally in the region of the axillary bud gaps. An examination of the region of the bud gap on unplanted cuttings revealed that although there was no complete break in the xylem cylinder its width was considerably reduced on the side of the bud with a corresponding increase in the width of the phloem. The xylem at this point contained a mass of wood rays densely filled with starch grains. Where the centre rays entered the phloem was an area of thin-walled parenchymatous cells containing less stainable contents that the surrounding cells (Fig. 12). After the cutting was planted a group of cells on the outward edge of this region enlarged and divided to form the root primordium (Fig. 13). Later the vascular system of the developing root became connected with the vascular system of the stem. There was no evidence of crushing

or distortion of the phloem on emergence, but increased pressure produced a break in the phellem before the final emergence of the root (Fig. 14).

SUMMARY.

The development of roots in hardwood cuttings of the gooseberry variety Keepsake was investigated by lifting samples of cuttings at intervals throughout the time of root formation. Roots occurred at points opposite the bud gaps on the stem and also just above the cutting base. The formation of either type of root was not dependent on callus production at the basal wound, but root development of both types was usually stronger on cuttings which had formed basal callus.

No pre-formed root initials were found in unplanted stems. Basal roots arose from areas of parenchymatous cells occurring near the cambium opposite a wood ray. Nodal roots arose from areas of parenchymatous cells near the cambium in the bud gap opposite an area of closely packed medullary ray cells which were filled with starch grains.

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BOOK REVIEWS

DISEASES OF GARDEN PLANTS. By A. BEAUMONT. (London : W. H. & L. Collingridge Ltd. 1956. Pp. 152, illus. Price 25s.)

The gardener who wishes to grow first-class crops must never be disheartened for he may have many disappointments which must be faced with composure. Not the least of his worries is the constant danger to his plants from the attacks of diseases about which keen gardeners continually seek advice from various sources. From time to time in recent years, books on the subject have been published but after reading the one by Mr. Beaumont most people will agree that none has yet dealt with this aspect of gardening in such detail.

In this book of eleven chapters, plus an index, the first contains a classification of common disease symptoms, devised by the author to help gardeners to identify signs of ill health. This is an important section because the early recognition of such troubles is of the utmost value if remedial measures are to be successful. The second chapter deals with the different methods in use for preventing or controlling various types of diseases according to whether they are carried on the seed, exist in the soil or spread through the air. Here we can learn about the latest chemical sprays and dusts in use as fungicides but many will be pleased to read that the old traditional Bordeaux mixture is still not to be despised and is even now regarded as a useful fungicidal spray. Mention is also made of the importance of breeding or selecting disease-resistant plants and of isolating newly purchased stocks for a while to make sure that virus disease is not present in them.

In the next nine chapters we can read about diseases of potatoes and other vegetables, of flowers, of trees and shrubs, of lawns and of different kinds of fruits. Plant names are used as headings and under each its different troubles are listed and described. For each the appropriate treatment is given—sometimes in brief but, where necessary, in detail. There is an admirable economy of words—the maximum amount of information being provided in the available space, while the search for it is not tedious. Numbers in brackets interspersed in the text make for easy cross-reference to comparable troubles on other plants and to suitable illustrations. There are no less than sixty-three photographs, most of which are of good quality, and there are sixteen line drawings showing spores of various parasitic fungi.

The advice given on chemical sprays and control treatments is as up-to-date as can be expected in these times when new discoveries arise so swiftly in most branches of science. For future editions, however, the author may take note of mistakes such as the wrong name for Crown Gall (p. 128) and the capitals in the specific names for the organisms causing Brown Rot and Eye Rot (p. 131). The fact that the trained pathologist may disagree with a sentence or two in the book need not deter any gardener from buying it. It has been written for him by a skilled plant pathologist who has had many years' experience in advising on plant disease problems and it contains a tremendous amount of useful information. It is an excellent reference book and the gardening enthusiast at the present day cannot buy a better one on the subject.

D.E.G.

DER OBSTBAU. Edited by G. FRIEDRICH. (East Germany, Neumann Verlag Radebeul, Schmincke-Allee, 19 : 1956. Pp. 736+12, illus.)

This large solid tome, compiled by the leading pomologists of Eastern Germany at Halle, Marquardt, Pillnitz and Leipzig, is slightly reminiscent of such earlier American manuals as *Fundamentals of Fruit Production* in that it affords information not only on individual practical problems of fruit growing but also on the scientific theory and knowledge on which good practice is based. Thus, the authors first consider in detail the anatomy, physiology and chemistry of the fruit plant before turning to the general problems of choice of rootstock, of pruning and of training. Environment, and in particular, as one might expect, frost incidence, receive their full share of attention. Separate sections concern planting schemes, the utilization of unfavourable sites, soil management, manuring, interculture, and soil sickness. Irrigation gets only brief mention. Picking, grading and packing are dealt with and also storage, with the emphasis on cold or cellar stores but with little on gas storage. Some thirty pages are devoted to plant protection measures and materials. Management questions, including costing and accounts, are discussed in some detail.

Probably the part that is likely to be of the most practical value to the English-speaking pomologist will be the 100 pages devoted to descriptions of the chief varieties of top and small fruits grown in Eastern Germany, with notes on their pollination needs and with attractive coloured plates of many apples and pears. Many of these varieties are already known elsewhere and others are perhaps worth knowing. Briefly, it seems to this reviewer that the average Anglo-Saxon fruit grower—if there be such a person—will naturally hesitate to buy good advice in a strange tongue, but the research worker, whose linguistic incapacity may in fact be comparable to that of the grower, will nevertheless be only too glad to thumb his way through relevant sections of this modern comprehensive reference work in his Institute's library, where undoubtedly it should find an honourable place.

D.A.

SOILS AND MANURES FOR FRUIT. Ministry of Agriculture Bulletin No. 107. (London : H.M. Stationery Office. 1956. Pp. 41, illus. Price 3s. 6d.)

The original edition of this bulletin (published in 1937) and its wartime successor (Growmore Bulletin No. 4) were published under the title " Manuring of Fruit Crops "; in the latest edition—also compiled by Professor T. Wallace of Long Ashton Research Station—the subject matter has not only been revised but considerably extended to include a section on soils for fruit, which summarizes some of the practical results of the Fruit Soil Surveys which have been carried out in the course of the last thirty years. In this section the author discusses the manurial relationships of the main soil groups on which fruit crops are grown and the soil requirements of the various fruits.

In the section dealing with the mineral requirements of fruits, the effects of deficiencies and excesses of the twelve essential mineral nutrients are fully described and advice is given on corrective treatment for these various deficiencies. The principles of manuring in relation to orchard practice are also discussed and details are given of the manurial treatments recommended for all the main fruits.

The bulletin is profusely illustrated with a series of thirty excellent photographs, twenty-three of which illustrate the types of nutrient deficiencies commonly found in fruit crops, and the remainder the growth effects of various soil series on apples.

T.E.W.

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1. The **Journal of Horticultural Science** is an official organ of the Horticultural and Agricultural Research Station, Long Ashton, Bristol, and the Horticultural Research Station, East Malling, Kent.

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